Dynamic Representations of the Body in Space

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Martin Riemer

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UNIVERSITÄT MANNHEIM

Dekan:	Prof. Dr. Michael Diehl
Erstgutachterin:	Prof. Dr. Herta Flor
Zweitgutachter:	Prof. Dr. Arndt Bröder
Vorsitz der Prüfungskommission:	Prof. Dr. Edgar Erdfelder
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Preface

The studies contained in the present thesis were conducted under financial support of the University of Mannheim, according to the *Landesgraduiertenförderungsgesetz* of Baden-Württemberg.

Chapter 2 and 4 (study 1 and 3) are revised versions of two articles published in *Experimental Brain Research* (Riemer, Trojan, Kleinböhl, & Hölzl, 2010; Riemer, Kleinböhl, Hölzl, & Trojan, 2013). Chapter 3 (study 2) is based on a manuscript submitted for publication in an international peer-reviewed journal. Chapter 5 (study 4), finally, contains a revised version of a manuscript intended for publication. For this reason, chapters 2-5 may also be read independently from each other.

The excerpt from the tale *Die erste Stunde nach dem Tode* by Max Brod (1916) on page 1 of the present thesis was translated by me to the best of my ability.

I want to thank Jörg Trojan, Dieter Kleinböhl and Rupert Hölzl for their professional support during my doctoral studies. Furthermore, I thank Anne-Kathrin Bräscher and all my other colleagues from the Otto-Selz-Institute for Applied Psychology at the University of Mannheim for a very pleasant and productive working atmosphere, and Jörg Jochims and Otto Martin for their technical support. Last but not least I thank my family and friends for their encouragement and help over the last three years. Particularly my parents Manfred and Erdmute Riemer deserve a special citation in this regard.

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1 General Introduction

"Don't you see", it resounded
piteously from above. "I've got
no sense of space, that's it.
Though I recognize rooms and
storeys, a certain kind of
regular arrangement of above
and below, of right and left, I
can't integrate this curious
arrangement with my senses, I
can't experience it intuitively..."

Max Brod (1916)

Spoken by a spiritual being after detachment from its physical body, these words symbolize the fundamental link between the experience of the own body and the experience of external space. Indeed, the body itself is phenomenally experienced as a spatial extension of our selves (James, 1890/1950; Metzinger, 2003), and the conception of perceived space without the conception of a perceiving self being located somewhere within that space is paradoxical. In his essay on the phenomenology of human consciousness, Jean-Paul Sartre pointed out that 'consciousness does not cease *to have* a body' (Sartre, 1943/1958, p.338). Postulating the absence of a physical body, the absence of any spatial extension of the phenomenal self, and thus the absence of the potentiality to affect (or be affected by) the external world, the emergence of a conscious percept of this external world would be absurd (Blanke & Metzinger,

2009; Gallese & Sinigaglia, 2010; Merleau-Ponty, 1945/1962; Sartre, 1943/1958). I cannot perceive space, unless *I* exist in space.[1]

The close connection between body and space representations enables an appropriate interaction with the environment (Eilan, Marcel, & Bermúdez, 1995; Legrand, Brozzoli, Rossetti, & Farnè, 2007; Merleau-Ponty, 1945/1962; van der Hoort, Guterstam, & Ehrsson, 2011). To manipulate and modify certain aspects of the external world by means of our body, we need information about the posture of our body and its physical capabilities, as well as information about the spatial relations of our immediate surroundings, commonly referred to as peripersonal space (Makin, Holmes, & Ehrsson, 2008; Spence, Pavani, Maravita, & Holmes, 2004). The representations of body and peripersonal space are so fundamentally linked that arguments striving for the fusion of both concepts have been raised (Cardinali, Brozzoli, & Farnè, 2009a; Legrand et al., 2007).

The present thesis deals with the dynamic qualities of body and space representations. It has been shown, that representations of body and space are not static, but exhibit remarkable dynamic capacities. Cortical reorganisation in patients after limb amputation (Elbert et al., 1994; Elbert et al., 1997; Yang et al., 1994), altered spatial processing induced by tool-use (Cardinali, Frassinetti, Brozzoli, Urquizar, Roy, & Farnè, 2009b; Iriki, Tanaka, & Iwamura, 1996; Longo & Lourenco, 2006; Maravita & Iriki, 2004; Yamamoto & Kitazawa, 2001) and perceptual disruptions during bodily illusions (Botvinick & Cohen, 1998; Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007; Lenggenhager, Tadi, Metzinger, & Blanke, 2007; Slater et al., 2009) are only some examples to indicate that the representations of the body and of peripersonal space are subject to many environmental influences. From an evolutionary perspective, the plasticity of body and space representations is advantageous and necessary, because an appropriate interaction with the environment depends on the adaptation to bodily changes, which happen during a lifetime necessarily and slow (growth, aging) as well as conditionally

[1] In this sentence, *I* refers to the phenomenal self, as space refers to phenomenal rather than material space, demonstrating that even the idealists' denial of the existence of any spatial extension beyond mental representations cannot minimize the interdependency between the phenomenal experience of body and space, which is independent from their factual existence.

and sudden (limb amputations, loss of sensory and/or motor functions due to nerve damage).

In the first part of this thesis (study 1 and 2), it was questioned to what extent the representation of peripersonal space is influenced by a postural representation of the body. Systematic variations of body posture were investigated with respect to their effects on the structure of spatial representations, which, as will be demonstrated, can be described in terms of a mental segmentation of peripersonal space.

The second part of the thesis (study 3 and 4) is dedicated to the identification of necessary and sufficient preconditions under which alterations of body representations occur. Although it is commonly recognized that body representations are flexible to a certain degree, the limiting factors for this plasticity are partially unknown. By varying the experimental methods to induce changes in body representations (see section 1.1), necessary prerequisites and limiting constraints regarding those changes are explored.

In short, the first part of the thesis deals with body representations as cause, while the second part is concerned with body representations as effects. In all four studies, bodily illusions were used to investigate the mechanisms of body perception. The next section (1.1) is therefore dedicated to the basic idea of this approach as well as to the description of the illusions used. Section 1.2 is destined to introduce and define important concepts and terms, which are essential for a complete understanding, section 1.3 gives a brief overview over the studies contained in this thesis and in section 1.4 I will shortly summarize the main objectives.

1.1 What We Can Learn from Bodily Illusions

The research on body representations is constrained by the fact that it is impossible to experimentally manipulate the presence or absence of the body. Every conscious and unconscious percept is inevitably accompanied by ‘the feeling of the same old body always there’ (James, 1890/1950, vol.1, p.242), rendering it impossible to compare the perception of the body with the perception under the

condition of an absent body (Tsakiris, 2010). Nevertheless, bodily illusions provide useful approaches to investigate some of the essential factors for the development and maintenance of body representations (Ehrsson, 2007; Geldard & Sherrick, 1972; Johannsen, 1971; Shore, Spry, & Spence, 2002; Tsakiris & Haggard, 2005).

The human brain is well adapted to its environment, and in most situations the corresponding body is appropriately represented, so that errors or malfunction can hardly be observed under normal conditions. However, to gain insights into the normal operating mode of body representations it is important to specify the conditions under which this normal functioning is disturbed (Johannsen, 1971). In the present thesis, tactile body illusions were implemented to induce specific disruptions of usual body perceptions. These deviations from the normal operating mode are a result of unfamiliar or even contradictive information (from various senses) about the body and its posture. The investigation of body perception under such conditions of reduced functionality is an enlightening strategy, because specific errors and malfunctions occurring under these conditions can reveal important insights about the usual functionality of body representations.

Prominent examples for tactile illusions are Aristotle's illusion (Johannsen, 1971) and the cutaneous rabbit effect (Geldard & Sherrick, 1972). Aristotle's illusion denotes the erroneous sensation of two objects, when in fact only one object is held between two crossed fingers of the same hand (Johannsen, 1971). In the cutaneous rabbit illusion, a rapid and regular sequence of tactile stimuli, the first half delivered near the wrist and the second half near the elbow, is perceived as being equally distributed between the two actual stimulation sites (Flach & Haggard, 2006; Geldard & Sherrick, 1972). Other perceptual impairments can be evoked by crossing the hands (Shore et al., 2002) or the feet (Schicke & Röder, 2006) or interleaving the fingers of both hands (Haggard et al., 2006; Zampini, Harris, & Spence, 2005). In a similar vein, hand posture was manipulated in study 1 and 2 in order to investigate the influence of a postural body model on the representation of peripersonal space.

Another well-established bodily illusion is the rubber hand illusion (RHI), first described by Botvinick & Cohen (1998). In the RHI, the own hand of the participant is concealed behind an

occluding screen, while direct vision at an artificial hand[2] is provided. The unseen real and the visible artificial hand are then stroked with two identical paint brushes in a synchronous manner, i.e., the felt touches at the own hand coincide with the seen touches at the artificial hand. In contrast to a control condition involving asynchronous stroking, this procedure results in the participants' illusion that they feel the touches at the observed artificial hand rather than at their veridical location. The illusory feeling that the artificial hand belongs to one's own body (usually assessed with a questionnaire) is accompanied by a shift of the perceived position of the own hand towards the location of the artificial hand. This perceptual bias is commonly referred to as proprioceptive drift (Costantini & Haggard, 2007; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009a; Tsakiris, 2010), and can be measured by asking the participants to indicate the perceived position of their own hand by pointing towards it with their non-stimulated hand (Botvinick & Cohen, 1998; Kammers et al., 2009a) or by verbal specification, e.g., with reference to a ruler placed horizontally above the hidden own hand (Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009b; Tsakiris, Prabhu, & Haggard, 2006).

An alternative version of the same paradigm involves synchronous as compared to asynchronous movements of the real and the artificial hand (Tsakiris et al., 2006). In contrast to the passive induction method, which results in the subjective feeling of ownership over the artificial hand, the active induction method is capable of inducing a sense of agency, because it is based on the sensory integration of motor commands and visual feedback about their effects (Tsakiris et al., 2006). In the present thesis, both versions of the RHI were directly compared in an attempt to disentangle the effects of body ownership and agency on different types of body representations (study 3), as well as their implications concerning a congenital body-model (study 4).

[2] The label 'rubber hand illusion (RHI)' dates from its first application by Botvinick & Cohen (1998), in which the artificial hand was made of rubber.

1.2 Clarification of Central Concepts

To provide a basis for a thorough comprehension of the studies contained in this thesis, it is appropriate to define some of the basic terms and concepts involved. The following sections are dedicated to this goal.

1.2.1 Body, Peripersonal Space and Response Fields

The distinction between the own body and the external world has a long history in philosophy and empirical sciences on the origin of human consciousness (Blanke & Metzinger, 2009; James, 1890/1950; Merleau-Ponty, 1945/1962; Sartre, 1943/1958; van der Hoort et al., 2011). The appropriateness of this distinction is implied by the fact that every conscious perception would be inconceivable without the reference to the first person perspective, the centre of which lies within the bodily borders (Blanke & Arzy, 2005; Lenggenhager, Mouthon, & Blanke, 2009). This first person perspective seems to be an absolutely necessary precondition for the development of a minimal phenomenal selfhood (Blanke & Metzinger, 2009; Metzinger, 2003; Zahavi, 2005). In other words, I cannot perceive an object 'per se', I can only perceive an object 'in front of me', 'far away from me', etc. Every perception[3] inevitably requires the reference to the first person perspective, and thus to the body (James, 1890/1950; Sartre, 1943/1958). These considerations imply that, in order to adequately interact with the external world, it is necessary to differentiate between representations of the own body (as the seat of the phenomenal self) and representations of external space (as the potentiality for actions) (Gallese & Sinigaglia, 2010).

Based on their functional relevance, the representation of external space can be further divided into near and far space (Legrand et al.,

[3] It might be important to differentiate between perception and imagination. The considerations discussed here only refer to directly perceived qualities of the external world. I refrain from taking up a position as to whether they are applicable to imaginations.

2007; Longo & Lourenco, 2007). Spatial areas, which are close to the body (and thus to the phenomenal self), are behaviorally more relevant and are represented differently compared to more remote spatial areas (Longo & Lourenco, 2006; Makin, Holmes, & Zohary, 2007). The research on different representations of near and far space resulted in the concept of peripersonal space, which is defined as the space immediately surrounding the body, i.e., within reaching distance (Holmes & Spence, 2004; Previc, 1998; Reed, Grubb, & Steele, 2006). Apparently, this definition strictly refers to the body itself. An altered representation of the body would necessarily imply a corresponding change in the representation of peripersonal space (Gallese & Sinigaglia, 2010), and indeed, the appropriateness of the distinction between the concepts of peripersonal space and body schema (see section 1.3.3) has been questioned (Cardinali et al., 2009a).

There have been many investigations highlighting the extensive dynamic qualities with respect to the representation of peripersonal space (Holmes, Calvert, & Spence, 2007; Longo & Lourenco, 2007; Lourenco & Longo, 2009; Maravita, Husain, Clarke, & Driver, 2001; Maravita, Spence, Kennett, & Driver, 2002). The majority of these studies were concerned about the effects of tool use on the extension of peripersonal space (Iriki et al., 1996; Longo & Lourenco, 2006; Maravita & Iriki, 2004) could show that the visual receptive fields of bimodal neurons in the brain of macaques were extended to more distant spatial areas, after a training to reach these areas with a rake. Behavioral correlates of this recalibration of peripersonal space have also been reported in human subjects (Longo & Lourenco, 2006; Maravita & Iriki, 2004).

The dynamics of peripersonal space are not confined to extensions and contractions of its range, but also affect the relative resolution of certain subdivisions within peripersonal space (Gillmeister & Forster, 2012; Lloyd, 2007; Làdavas, di Pellegrino, Farnè, & Zeloni, 1998; Reed, Betz, Garza, & Roberts, 2010; Short & Ward, 2009; Whiteley, Spence, & Haggard, 2008). So are the spatial areas immediately surrounding the hands, often referred to as peri-hand space, overrepresented compared to other spatial areas within peripersonal space (Brozzoli, Gentile, & Ehrsson, 2012; Làdavas & Farnè, 2004; Makin et al., 2008; Reed et al., 2006; Reed et al., 2010). Again, this irregular resolution of spatial representations can be

explained in terms of a different behavioral relevance (Brozzoli et al., 2012; Reed et al., 2006).

All of these studies demonstrate that the dynamics of peripersonal space representations are closely related to variations of body posture (especially regarding the hands) and to attentional processes (Driver & Grossenbacher, 1996). In study 1 and 2 of the present thesis, this relation will be further investigated, and a hypothesis concerning a mental segmentation of peripersonal space into response fields will be tested. Response fields are defined as spatial subdivisions, representing specific body parts. A mental segmentation of peripersonal space into response fields was hypothesized to facilitate the tactile processing of body parts, because the identification of a touched body part would only require the localization of the tactile stimulus within a specific response field (representing the associated body part), rather than a supplemental determination of the body part currently occupying the same spatial area. An example of response fields and their dependence on body posture is described in the introduction of study 1 and depicted in Figure 1. Based on the results of study 1 and 2, response fields are proposed as a conceptual framework for the investigation of tactile processing of body parts within an external reference system.

1.2.2 Ownership and Agency

The distinction between a sense of body ownership and a sense of agency as two different aspects of the bodily self has received much interest during the last decade (Gallagher, 2000; Tsakiris, Schütz-Bosbach, & Gallagher, 2007b). The function of the human body as the mediating interface between the phenomenal self and the external world is twofold (Merleau-Ponty, 1945/1962).

First, the body is perceived as the source of sensations. An externally imposed event at the body directly results in a phenomenal sensation of that event, the body being the only medium by which the external world can exert its influence upon the phenomenal self. Contact between a knife and an object on my desk would have no

consequences for my phenomenal self[4], but if the same knife approaches my hand, the anticipation of the phenomenal consequences would immediately make me feel uncomfortable. This aspect of a bodily self-consciousness is commonly referred to as body ownership, reflecting the sense that whatever happens to this body, happens to *me* (within the meaning of the phenomenal self).

Second, the body is perceived as a medium to manipulate and modify the external world. Intended changes within the environment can only be imposed by means of motor control over the body. For all intents and purposes, the influence of the phenomenal self upon the external world is indirect, mediated by the body. In order to move the knife on my desk, I first have to reach for it with my hand, whereas the body movement itself can be executed directly[5]. This second aspect of bodily self-consciousness is termed agency and describes the sense that *I* can affect my environment only via this body.

Body ownership and agency both result in a strongly perceived association between the body and the phenomenal self, and, in this vein, contribute to the development of a bodily self (Gallagher, 2005; Merleau-Ponty, 1945/1962).

The distinction between body ownership and agency has stimulated numerous empirical investigations (Kalckert & Ehrsson, 2012; Kammers et al., 2009b; Longo & Haggard, 2009; Tsakiris et al., 2006; Tsakiris, Longo, & Haggard, 2010) as well as theoretical considerations (Gallagher, 2000; Tsakiris et al., 2007b), but the interrelation between both concepts remains an unresolved question. Some studies suggest them to be disjunctive aspects of the bodily self, absolutely independent from each other (Synofzik, Vosgerau, & Newen, 2008; Tsakiris et al., 2010), while others favour an additive model, proposing a common basis sufficient for ownership and

[4] For the sake of simplicity and due to the objective of this thesis, the example is restricted to somatosensation. Of course, other senses (e.g., vision) are not reliant on bodily contact, and can transfer remote external events to alterations in the phenomenal self. However, even those events are perceived from the first-person perspective of the body. Regarding vision, I do not perceive a knife approaching an object, but a knife approaching an object *far away from me*.

[5] The fact that motor intentions and body movements are also mediated by efferent nerve pulses does not derogate the argument of phenomenal immediacy, because those mediating processes are not consciously perceived. Phenomenal immediacy is even regarded as an essential precondition to enable adequate motor control (Prinz, 1992; Sartre, 1943/1958).

necessary for agency and a supplementary condition necessary for the development of agency (Gallese & Sinigaglia, 2010). According to this latter view, body ownership can be maintained without a sense of agency, whereas agency would necessarily imply a sense of ownership. Indeed, there are some clinical syndromes (anarchic hand syndrome, delusions of control in schizophrenic patients) reflecting the case of a disturbed sense of agency coincidentally with a preserved sense of ownership (Frith, 2005; Marchetti & Della Sala, 1998), while there are no reports of the reversed case (disrupted ownership with preserved agency)[6]. Nevertheless, arguments for the independence hypothesis are provided by the observation of distinct neural networks activated during the induction of ownership and agency (Tsakiris et al., 2010).

Irrespective of the relation between ownership and agency, it has been shown that they affect the perception of the body in a qualitatively different manner. By comparing the perceptual effects of passive tactile stimulation and active finger movements within the RHI, Tsakiris et al. (2006) found that the perceived spatial displacement was restricted to the stimulated finger in the passive induction method, while it was spread over the whole hand in the active induction method. Voluntary control over the movements of an artificial hand, giving rise to the emergence of agency, seem to have a more widespread effect on body representations, whereas tactile stimulation seems to exclusively affect the touched body part (Tsakiris et al., 2006).

Based on these results, it is plausible to assume a greater importance of the anatomical congruence between motor commands and their bodily effects (resulting in a sense of agency) than between tactile stimuli at the body and their sensory consequences (resulting in a sense of ownership), a hypothesis which was tested in study 4 of the present thesis.

[6] Somatoparaphrenia might be a candidate, but it co-occurs with motor and somatosensory deficits, impeding the assessment of agency (Vallar & Ronchi, 2009).

1.2.3 Body Image and Body Schema

Since the original conceptualization by Head & Holmes (1911) the distinction between two different kinds of body representations has been confirmed in various studies and is generally approved in the scientific literature (de Vignemont, 2010; Gallagher, 2005; Kammers et al., 2009a; Paillard, 1999). Based on clinical observations of discrete functional deficits in neurological patients, Head & Holmes (1911) proposed the existence of at least two body representations, which are commonly referred to as body image and body schema[7] (Gallagher, 2005).

The body image contains the sum of conscious perceptions and attitudes towards one's own body, and is accompanied by a high level of consciousness. The content of the body image varies with the attention towards specific aspects or parts of the body, i.e., it does not consist in a holistic representation, but rather in 'an abstract and partial perception of the body' (Gallagher, 2005, p.57).

The body schema refers to a pre-conscious representation of the body serving as an implicit frame of reference for the execution and guidance of goal-directed movements, which usually do not require conscious monitoring (e.g., walking, grasping objects, etc.). It is described as a 'combined standard, against which all subsequent changes of posture are measured before they enter consciousness' (Head & Holmes, 1911, p.187). Accordingly, the body schema operates within an external frame of reference, i.e., behaviorally relevant visual information and bodily sensations are processed with respect to their coordinates in peripersonal space. The extent to which specific body parts (e.g., hands and fingers) are included in this spatial body representation was investigated in study 1.

The conceptual distinction between body image and body schema is confirmed by a double dissociation revealed by clinical case studies (Gallagher, 2005; Head & Holmes, 1911). Deafferentation, a neurological condition indicating the loss of somatosensation and proprioception from the neck downwards due to nerve damage, forms one side of this dissociation, i.e., the case of a disturbed body schema, while the body image is preserved (Cole & Paillard, 1995;

[7] The original term introduced by Head & Holmes (1911) is 'postural schema'. According to conventions in the more recent literature, the established term 'body schema' will be used here.

Gallagher & Cole, 1995; Paillard, 1999). Unilateral neglect and tactile blindsight are examples for the reversed pattern, the coincidence of a defective body image and an intact body schema (Gallagher, 2005; Paillard, 1999; Rossetti, Rode, & Boisson, 1995).

Based on the distinction between a sense of ownership and a sense of agency (see section 1.3.1), Kammers et al. (2009b) suggested that these two aspects of the bodily self should differently affect the body image and the body schema. The body image (in contrast to the body schema) should be modifiable by manipulating the sense of body ownership, because the feeling of ownership is elicited by passively experienced tactile sensations and is not associated with movements. This is exactly what was found in another study by the same group (Kammers et al., 2009a), although the proposed influence of a sense of agency on the body schema could not be confirmed (Kammers et al., 2009b). The absence of body-schematic alterations after the experimental manipulation of agency, however, might be due to the experimental design, because in the study of Kammers et al. (2009b), as in many others (Longo & Haggard, 2009; Newport, Pearce, & Preston, 2010; Tsakiris et al., 2006), agency was induced over a spatially displaced video-image of the participants' real hand, which presumably is very different from inducing agency over an unequivocally body-extraneous object (Kalckert & Ehrsson, 2012). Study 3 of the present thesis focuses on this issue by implementing a version of the RHI based on active motor control over an unambiguously artificial hand.

1.2.4 Congenital Body-Model

A critical issue with respect to body representations consists in the question whether the way we perceive our body develops in early childhood depending on postnatal learning mechanisms or whether it is based on a congenital default model of the human body, also referred to as pre-existing body-model (De Preester & Tsakiris, 2009). The discussion about the existence and the plasticity of a congenital body-model has a long history in the research on body perception, yet it still remains undetermined. The reason for its

intricacy apparently stems from the fact that there is convincing evidence for both the rigidness and the plasticity of body representations, which will be exemplified in the following.

The phenomenon of aplasic phantoms, i.e., the perception of phantom sensations from congenitally deficient limbs, highly suggests the existence of a congenital body-model (Brugger et al., 2000; Gallagher, Butterworth, Lew, & Cole, 1998; Ramachandran, 1993). These phantom sensations can occur during the whole life-span of the patients, in spite of the absolute absence of any sensory afferences from the respective limb (Melzack, Israel, Lacroix, & Schultz, 1997). These clinical cases show that the subjective experience of a body part does not necessarily depend on sensory-motor contingencies regarding the specific body part. The anatomical configuration of the body seems not to be learned, but to be congenitally available and resistant to inconsistent sensory information. Although these clinical observations reinforce the conception of a congenital body-model, alternative explanations for the phenomenon of aplasic phantoms have been proposed (Price, 2006).

Further evidence for a congenital body-model is provided by experimental studies, revealing several anatomical constraints regarding the alteration of body representations (Costantini & Haggard, 2007; Ehrsson, Spence, & Passingham, 2004; Graziano, Cooke, & Taylor, 2000; Haans, Ijsselsteijn, & de Kort, 2008; Holmes, Snijders, & Spence, 2006; Pavani, Spence, & Driver, 2000; Tsakiris & Haggard, 2005). Several examples indicate that the temporal synchrony between tactile and visual stimulation is, though a necessary, not a sufficient factor for the occurrence of the RHI (Tsakiris, 2010). The effects of the illusion have been shown to vanish, when the artificial hands were arranged in an anatomically impossible posture (Ehrsson et al., 2004; Pavani et al., 2000; Tsakiris & Haggard, 2005), and to be substantially diminished, when the artificial hands were replaced by neutral, body-unrelated objects (Haans et al., 2008; Holmes et al., 2006; Tsakiris & Haggard, 2005; but see Armel & Ramachandran, 2003). These findings demonstrate that specific anatomical attributes of the artificial hand are required for the RHI, and that the perceived incorporation of body-extraneous objects depends on *a priori* conceptions regarding the anatomical structure of the human body.

Other studies, however, illustrate a considerable flexibility of body representations, even beyond the limits of anatomical discrepancies (Armel & Ramachandran, 2003; Braun et al., 2001; Guterstam, Petkova, & Ehrsson, 2011; Moseley & Brugger, 2009; Schaefer, Flor, Heinze, & Rotte, 2007; Schaefer, Heinze, & Rotte, 2008; Schaefer, Heinze, & Rotte, 2009). In a series of brain imaging studies, Schaefer et al. (2007; 2008; 2009) could show that bodily illusions, induced by visual exposure to an altered configuration of the body, modulated the topography of the primary somatosensory cortex. Most importantly, these short-lived alterations in the primary somatosensory cortex occurred after visual exposure to anatomically implausible (e.g., a lengthened arm, Schaefer et al., 2007) and even anatomically impossible bodily changes (e.g., a third arm, Schaefer et al., 2009; see also Guterstam et al., 2011).

Further evidence for the plasticity of body representations is provided by experiments on tool-use. After a certain period of handling a tool, altered representations of the body have repeatedly been reported (Cardinali et al., 2009b; Cardinali et al., 2011; Yamamoto & Kitazawa, 2001). The original conceptualization of the body schema already highlights the capability of projecting the sense of posture and movement 'beyond the limits of our own bodies to the end of some instrument held in the hand' (Head & Holmes, 1911, p.188). The perceptual and behavioral effects of tool-use vividly demonstrate the impressive dynamic qualities of body representations (De Preester & Tsakiris, 2009; Head & Holmes, 1911; Johnson-Frey, 2003; Longo & Lourenco, 2006; Maravita & Iriki, 2004).

In summary, body representations definitely exhibit a certain degree of flexibility, but they are not unlimited. As mentioned initially, the constraints on the plasticity of body representations has generated the assumption of a congenital body-model (De Preester & Tsakiris, 2009; Tsakiris & Haggard, 2005). The fact that body-schematic alterations after tool-use depend on the active manipulation of the tool suggests a high involvement of motor processes. The importance of the motor system for representational changes of the body has also been shown in other studies (Braun et al., 2001; Moseley & Brugger, 2009; Schaefer, Flor, Heinze, & Rotte, 2005). Therefore it is possible that the influence of a congenital body-model depends on whether alterations of body representations are induced by active voluntary movements or by

passive tactile sensations. In study 4 of this thesis, this issue was investigated by comparing the effects of anatomically incongruent feedback within a passive and an active version of the RHI (see section 1.1).

1.3 Overview of the Studies

The present thesis deals with the questions (i) to what extent postural body representations modulate the representation of peripersonal space and (ii) to what extent body representations can be modulated by spatially displaced visual feedback regarding passive touches at the body and active movements of the body. This section is designed as a brief common overview of the four studies and might be helpful for a first overall impression. However, it does not intend to provide a comprehensive description of the studies' details, for which the reader should consult the respective chapters.

Study 1 It was examined whether the tactile processing of body parts was modulated by postural representations of the body. Participants received tactile stimuli at the fingertips of their index and middle fingers while holding their hands either in a vertical or a woven posture (Figure 1) and were asked to discriminate as fast as possible either between stimuli at their right vs. left hand, or between stimuli at their index vs. middle fingers. Besides the contribution to the controversially discussed question as to whether single fingers are included in a postural representation of the body, study 1 set the basis for the hypothesis of response fields.

Study 2 We tested three characteristics of response fields, which were proposed on the basis of the results from study 1. Again, tactile stimuli were applied to the fingertips of the participants' index and middle fingers, while participants had to identify the laterality of the stimulated hand. In experiment 1, hands were held in an adjacent or a separated posture (Figure 6a), modulating the spatial distance between response fields for the right and the left hand. In experiment 2 and 3, participants held their hands in a right-enclosed or a left-

enclosed posture (Figure 7a), varying the size and the number of response fields. Although the results of study 2 confirmed the basic idea of response fields, an important modulation regarding the characteristics of size and number was brought forward.

Study 3 By presenting spatially displaced visual feedback regarding passive tactile stimuli at (or active movements of) the participants' right index finger within the paradigm of the RHI, we investigated the relative contribution of a sense of ownership and a sense of agency with respect to changes in body representations. Effects on body representations were assessed by phenomenal self-reports, a perceptual and a behavioral measure of proprioceptive drift. Study 3 was designed to disentangle alterations of the body image and the body schema (see section 1.2.3).

Study 4 It was investigated whether the influence of a congenital body-model (see section 1.2.4) differs depending on the induction method for the RHI. Passive tactile stimuli at (or active movements of) the participants' right index and middle finger were accompanied by visual feedback at an artificial hand. The visual feedback was varied according to its anatomical congruence (whether anatomically corresponding fingers at the real and the artificial hand were stimulated or moved) and coupling consistency (whether the coupling between real and artificial fingers varied).

1.4 Aims and Scope

In this section, the main research questions of the present thesis as well as methodological aims are summarized.

1.4.1 Dynamics of Spatial Representations

The first part of the thesis (study 1 and 2) is concerned with the influence of body posture on the representation of peripersonal space (see section 1.2.1). A mental segmentation of peripersonal space into task-relevant subdivisions was hypothesized to account for the spatial processing of tactile stimuli within an external reference system. This mental segmentation of space was expected to depend on the postural representation of the body as well as on the amount of attentional resources focused on specific body parts. The hypothesis was tested in study 1, resulting in the conceptualization of response fields. The primary goal of study 2 consisted in the validation and further elaboration of response fields, which will be discussed as a conceptual framework for the processing of tactile stimuli within an external frame of reference.

1.4.2 Dynamics of Body Representations

A central concern of the second part of the thesis (study 3 and 4) was to determine necessary preconditions as well as limiting factors for alterations of body representations. Several factors were tested regarding their capability to induce the RHI, the subjective embodiment of an artificial hand.

Specifically, we examined the influence of top-down processes on the occurrence and the strength of the RHI. In many studies on the RHI (especially those implementing active movements) video

images or mirror reflections of the own hand were presented as 'artificial' hands, which raises issues as to whether the perceptual incorporation of these images can be accounted for solely by top-down processes. In fact, the participants *are* looking at their own hand, though the image is spatially displaced. To test for this possibility, an unambiguously body-extraneous object (a movable wooden hand) was used in study 3 and 4.

The assumption of a congenital body-model (see section 1.3.4) predicts the importance of an anatomically congruent coupling between fingers at the real and the artificial hand as a necessary precondition for the RHI. Similar anatomical constraints have been reported in other studies (Ehrsson et al., 2004; Haans et al., 2008; Holmes et al., 2006; Pavani et al., 2000; Tsakiris & Haggard, 2005). In study 4 the impact of anatomical congruence was tested against the impact of the consistency of this coupling.

1.4.3 Body Ownership and Agency

The distinction between a sense of body ownership and a sense of agency (see section 1.2.2) implicates different processing strategies for passive tactile sensations at and active voluntary movements of the own body. The investigation of this issue was another aim of this thesis.

Study 3 examined differential effects of passive touch and active movements within the RHI on the body image and the body schema (see section 1.2.3). In order to disentangle alterations specific for these functionally different body representations, we compared the performance in a perceptual task (presumably based on the body image) with that in a motor task (presumably based on the body schema). This question was addressed previously by Kammers et al. (2009b), but due to the implementation of an advanced method for the induction of the RHI in study 3 (see next paragraph on methodological aims) further informative results were expected, and firmer conclusions could be drawn.

In study 4 we assessed the differential impact of a congenital body-model with respect to the development of a sense of body

ownership as compared to a sense of agency. The importance of anatomical congruence of the coupling between fingers of the real and the artificial hand was compared for passive touches and active movements within the RHI.

1.4.4 Methodological Aims

The present thesis involved two methodological objectives, the first of which consisted in the implementation of a new procedure for the RHI paradigm based on active motor control over an unambiguously artificial hand. To enable voluntary movements of artificial hands, many authors used video-based (e.g., Tsakiris et al., 2006) or mirror-based (e.g., Holmes et al., 2006) versions of the RHI, which seem questionable when the object of investigation is the perceived incorporation of an *artificial* hand, definitely *not* belonging to the own body. The general principle of the new method was validated in study 3 and it was applied and further elaborated in study 4.

Second, a new procedure for the assessment of proprioceptive drift within the RHI was implemented and validated in study 3, allowing for the calculation of a parameter for discrimination performance. This procedure is the first to enable the specification of the degree of certainty for judgements about body posture, an aspect of the RHI which has not been considered in previous studies. This procedure was successfully applied in study 3 and 4.

2 Study 1: A Mental Segmentation of Peripersonal Space Depends on Body Posture

It is an unresolved question whether single fingers are represented within a spatial frame of reference. The two experiments in study 1 investigated the impact of postural representations of the body on the processing of tactile stimuli at the fingers and hands.

Healthy subjects received two simultaneous tactile stimuli at the fingertips while the fingers of both hands were either interleaved or not. In speeded response tasks, they were asked to discriminate (experiment 1) or to identify (experiment 2) the touched body parts, either regarding hand laterality or finger type. The results demonstrate that both finger discrimination and finger identification are influenced by body posture. We conclude that the assumption of a solely somatotopic representation of fingers is not tenable and that an external reference system must be available for the processing of tactile stimuli at the fingers. The results are discussed in terms of a mental segmentation of peripersonal space, based on a postural representation of the body and task requirements.

2.1 Introduction

Tactile stimuli can be localized within somatotopic and external frames of reference (Azañón & Soto-Faraco, 2008; Head & Holmes, 1911; Kim & Cruse, 2001). These two reference systems differ in their dependence on body posture. While the somatotopic coordinates of specific body parts do not change with different postures of the body, their external spatial coordinates do (Driver & Grossenbacher, 1996; Kitazawa, 2002; Lloyd, Shore, Spence, & Calvert, 2003; Pellijeff, Bonilha, Morgan, McKenzie, & Jackson,

2006; Röder, Spence, & Rösler, 2002; Shore et al., 2002; Soto-Faraco, Ronald, & Spence, 2004).

Many studies have addressed the question whether hands and fingers can be processed within an external reference system (Azañón & Soto-Faraco, 2007; J. C. Craig, 2003; Haggard et al., 2006; Schicke & Röder, 2006; Schicke, Bauer, & Röder, 2009; Shore et al., 2002; Shore, Gray, Spry, & Spence, 2005). There is agreement about the representation of the hands' posture in external coordinates, but the findings concerning such a representation of single fingers are inconsistent. Many authors doubt the integration of single fingers within an external frame of reference, referring to illusory perceptions like Aristotle's illusion, which is the deceptive feeling of two objects when actually only one object is held between two crossed fingers (Johannsen, 1971). This illusion has repeatedly been interpreted as reflecting the brain's inability to update the fingers' posture relative to each other (Benedetti, 1985; Benedetti, 1988). Indeed, in some studies no postural influence on finger processing was found (Benedetti, 1985; Benedetti, 1988; Haggard et al., 2006). Other investigations, however, provided evidence that finger processing is affected by body posture (J. C. Craig & Busey, 2003; J. C. Craig, 2003; Shore et al., 2005).

In an attempt to resolve the inconsistencies on this issue we identified three aspects, which have to be accounted for when investigating hand and finger representations in peripersonal space: task comparability, information value and the spatial distance between related body parts. These three aspects will be specified in the following.

The first aspect relates to the comparability of the experimental tasks. In order to compare between hand and finger processing, it is important to ensure the analogousness of the experimental tasks. Ideally, they should differ only with respect to task instructions (i.e., whether attention is directed to the distinction of hands or to the distinction of single fingers). Therefore, an excellent method is provided by the analysis of the processing strategies of tactile stimuli applied to the fingertips. This approach allows direct comparison of hand and finger representations, because one and the same stimulus can be processed both with respect to hand laterality and finger type (i.e., index, middle) (Haggard et al., 2006).

The second aspect consists in the reduction of uncertainty regarding the stimulus' location in peripersonal space. In terms of

information value (Gigerenzer & Murray, 1987; McFall & Treat, 1999), distinguishing between the hands provides much more spatial information than distinguishing between finger types. Having identified the laterality of a touched hand, we can specify the stimulus' location within the space near that hand, even if the touched finger remains unknown. In contrast, identification of the touched finger type, without taking into account the laterality of the associated hand, confronts us with more uncertainty regarding the stimulus' external coordinates. Given a possibly larger distance between two fingers of the same type (i.e., between two hands), the stimulus cannot be constrained to a circumscribed area in peripersonal space. Its location might differ highly depending on the associated hand. Thus, when touched at a specific finger, humans might automatically process the laterality of the associated hand, even if they are explicitly asked to ignore it. Similar effects of task-irrelevant information have frequently been reported in various studies (Simon & Acosta, 1982).

The third aspect is the spatial distance between related and unrelated body parts (determined by task demands). Within an external frame of reference, tactile stimuli are localized with respect to external spatial coordinates (Azañón & Soto-Faraco, 2007; Azañón & Soto-Faraco, 2008; Kitazawa, 2002). By determining the part of the body which is currently occupying that space, one can infer the stimulated body part. In order to identify the laterality of a touched hand, it would be beneficial to mentally subdivide peripersonal space into two discrete areas, defined by the position of the hands. Each area would then represent one of the two response alternatives (i.e., the right or the left hand). Such a mental segmentation of peripersonal space would facilitate performance, because hand identification would only require the distinction of two discrete spatial areas and the localization of the stimulus within one of these areas. The spatial proximity of fingers of the same hand, as well as the spatial distance between fingers of different hands might serve as a basis for a better identification of hands within an external reference frame (Driver & Grossenbacher, 1996; Kim & Cruse, 2001; Shore et al., 2005; Soto-Faraco et al., 2004). Changing the task requirements from hand to finger processing, the same principles would suggest a perceptual advantage for other postures: fingers of the same type should be spatially close to each other, while fingers of different types should be spatially distant.

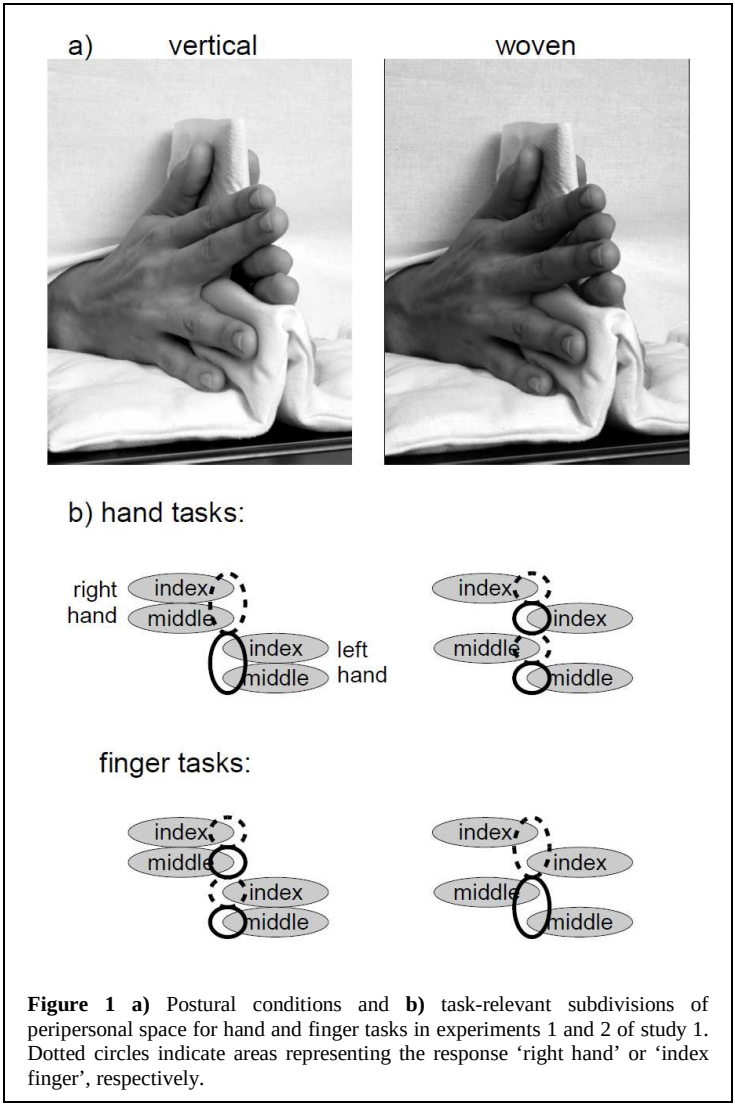

Figure 1 a) Postural conditions and **b)** task-relevant subdivisions of peripersonal space for hand and finger tasks in experiments 1 and 2 of study 1. Dotted circles indicate areas representing the response 'right hand' or 'index finger', respectively.

The effects of the spatial distance between related and unrelated fingers can be investigated by the experimental modification of hand postures (Driver & Grossenbacher, 1996; Kim & Cruse, 2001; Shore et al., 2002; Shore et al., 2005; Soto-Faraco et al., 2004). A sound method is to compare a posture, in which the fingers of both hands are interleaved, and a posture, in which the fingers are ordered according to the associated hand. Variations of these postural conditions have been implemented in several studies (Haggard et al., 2006; Röder et al., 2002; Zampini et al., 2005). Another example, restricted to index and middle fingers of both hands, is depicted in Figure 1a.

The postulated segmentation of peripersonal space into task-relevant areas is differently affected by the vertical and the woven posture, depending on task requirements (Figure 1b). Regarding hand processing, related fingers are adjacent in the vertical, but not in the woven posture. The former allows the mental construction of two discrete areas, while in the latter hands cannot clearly be assigned to one spatial area each, because these are overlapping. Each hand is no longer represented by one broad, connected area, but by two smaller ones, which are separated by areas occupied by fingers of the other hand. This relation is reversed for finger processing, because here it is the woven posture in which related fingers are adjacent (Figure 1). According to these considerations, we assume that processing of hand laterality would be facilitated during the vertical posture, while processing of finger type would profit from the woven posture.

However, in a recent study by Haggard et al. (2006), a postural effect was found only for the processing of hands. Participants received single tactile stimuli at their fingertips and were asked to indicate the laterality of the stimulated hand or the type of the stimulated finger, respectively. While hand identification was indeed enhanced during the vertical as compared to the woven posture, no perceptual advantage was found for finger identification, neither during the vertical nor the woven posture (Haggard et al., 2006). This finding was interpreted as contradicting the representation of single fingers within an external reference system.

Our considerations about information value and the hypothesized converse effects of the postural conditions regarding hand and finger processing suggest an alternative explanation for the absence of a

postural effect on finger identification in Haggard et al. (2006). Due to implicit hand processing during the finger task, the facilitating effect of the woven posture on finger identification could have interfered with the impeding effect of the same postural condition on hand identification. Similarly, a decrease in finger identification performance during the vertical posture may have been obscured by improved hand identification during that posture. Advantageous and disadvantageous effects could have compensated for each other, thereby concealing any postural influences on the finger identification task.

In the present study we investigate the effects of the vertical and the woven posture on tactile processing of hands and fingers. We claim that single fingers can be processed within an external frame of reference, and that the woven posture facilitates finger processing. Both experiments of the present study were conducted as an attempt to suppress implicit hand processing during the finger task and to seek evidence for postural influences on the processing of single fingers.

2.2 Experiment 1

In experiment 1, two tactile stimuli were applied synchronously to the tips of the index fingers and the middle fingers of both hands, while participants were adopting one of two postural conditions. In the vertical posture, index and middle finger of the right hand were placed vertically above the ones of the left hand. In the woven posture, index and middle fingers of both hands were interleaved, with the right index finger on top (Figure 1a). Participants were asked for equality judgements, i.e., they had to determine whether the stimuli were applied to the same or to different hands, in the hand discrimination task[8], and to the same or to different finger types, in the finger discrimination task, respectively.

[8] The difference between equality judgements and explicit naming of body parts (or categories of body parts) consists in the need for exact identification. Equality judgements do not require identification, but instead can be based solely on the discrimination of body parts. To account for these deviant requirements we will

The experimental tasks are based on those implemented by Haggard et al. (2006), but vary in three details. These three details are related to the three important aspects concerning investigations of hand and finger processing in peripersonal space, namely task comparability, information value and the spatial distance between related fingers.

First, each trial consisted of two simultaneously delivered stimuli rather than one, and participants were asked for equality judgements concerning these stimuli rather than for identification of a touched body part. This method was applied by Haggard et al. (2006, exp. 2) only for the hand task. The essential consequence of this modification relates to the information value of hand and finger processing. Supplemental hand processing during the finger task provides no incremental information concerning the external location of the stimuli, since targets (i.e., stimulation of both fingers of the same type) involve the stimulation of both hands anyway. Furthermore, due to the adjustment of response modes ('same/different' in both tasks rather than 'right/left' in the hand task and 'index/middle' in the finger task) the task comparability is enhanced.

Second, stimulation was restricted to the index fingers and the middle fingers of both hands, as in experiment 4 of Haggard et al. (2006). This constraint yields considerable advantages for the comparability of the areas that are occupied by related fingers during both tasks (Figure 1b). Moreover, task comparability is warranted by equal numbers of possible stimulus combinations between the tasks (Figure 3).

Third, only index and middle fingers were arranged according to the postural conditions (Figure 1a). Hence, in the vertical posture the right middle and the left index finger were adjacent, rather than being separated by ring and little finger of the right hand, as it has been the case in Haggard et al. (2006). As a consequence, the spatial distance between the four relevant fingers is equal for both postural conditions, though the configuration of task-related subdivisions of peripersonal space is inversely affected by them (Figure 1b).

According to our considerations about a mental segmentation of peripersonal space, we hypothesized a facilitating effect on finger

distinguish between identification and discrimination tasks. According to this label distinction, identification tasks were used in Haggard et al. (2006, except exp. 2) while we will implement discrimination tasks in experiment 1.

discrimination during the woven posture, when homologous fingers are adjacent to each other. Enhanced performance for finger discrimination during the woven posture would strongly suggest a processing of fingers within an external reference system. In contrast, if fingers are only processed within a somatotopic frame of reference, no postural effect should be observable in the finger discrimination task.

More precisely, for the hand discrimination task, we hypothesized shorter reaction times and fewer errors during the vertical as compared to the woven posture. For the finger discrimination task, shorter reaction times and fewer errors were expected during the woven as compared to the vertical posture.

2.2.1 Methods

Participants Twelve healthy participants, recruited from the University of Mannheim and from the local community, took part in the study. They were either paid for their participation or received credit points for participating in an experiment (for psychology students). Data from one participant had to be excluded from the analyses because of problems in the technical set-up. Mean age of the remaining eleven participants (4 males) was 24.4 years. All but one were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave written informed consent to the experiment.

In addition to the assessment of handedness, participants were asked about past injuries at the hands or fingers (e.g., bone fractures) as well as about frequent activities involving precise finger coordination (e.g., playing musical instruments). All reported injuries (18%) were completely healed, and six participants had been playing musical instruments for at least five years.

Experimental set-up Participants were seated in front of an occluding screen, which deprived them of the view of their hands. The hands rested comfortably on pillows, in a manner that allowed only the index and the middle fingers to reach the body midline. The

other fingers and the thumbs were placed at the ipsilateral side and were prevented from getting in touch with their counterparts on the contralateral hand (Figure 1a).

Tactile stimuli were delivered via miniature solenoids (RS Components, model 330-5213) attached to the fingertips with thin strips of adhesive tape. To enable the solenoid pins to swing back to their original position after stimulation, plastic nuts with a width of 4mm were fixed between the solenoids and the skin of the fingertips, thus keeping a constant distance. Stimulus duration was set to 20ms, which was sufficient to induce a well-noticeable tactile sensation. Active noise-cancelling headphones (Audio Technica ATH-ANC7, QuietPoint®) were used to reduce acoustic disturbance caused by the solenoids.

Motor responses were given via two foot pedals, one of them indicating a 'same' and the other one indicating a 'different' judgement. The lateral meaning of the foot pedals was randomized across subjects. Within subjects, the denotation of the foot pedals was kept constant during the experiment, in order to avoid confusion. Visual reminders with verbal descriptions of their meaning were attached to the occluding screen.

The tasks were presented in randomized order. The order of the two postural conditions was randomized only within the respective task, so that each task was accomplished successively in both postures. This constraint should reduce confusion due to the changes in task requirements. Each block consisted of 60 single trials, so each of the six possible stimulus combinations (Figure 3) was applied ten times in randomized order. The intertrial interval between the subjects' response and the onset of the following stimulus combination was approximately normally distributed within a range of three to five seconds. Stimulus sequences were controlled using Presentation v12.2 (Neurobehavioral Systems, Inc., CA, USA).

Previous to each block, the experimenter helped the participants to arrange their hands in the correct manner. Participants were instructed about the type of the following task (finger vs. hand discrimination) and were asked to respond as accurately and as quickly as possible. Participants were told to keep their eyes open and to focus on a black cross, which was fixed to the occluding screen in front of them.

We tested for mechanical transmission of the tactile stimuli, i.e., the possibility that the impulses caused by the solenoids are carried

over from the stimulated to adjacent fingers. Participants interleaved their hand with that of a second person and stimuli were applied only to the second person's fingers. A slight tremor spreading from stimulated to adjacent fingers occurred, which was very low but, in the absence of direct stimulation, could be reliably detected (100%). Yet, during the whole length of the experiment, all participants consistently reported the perception of exactly two touches per trial, indicating that mechanical transmission did not interfere with the perception of the stimuli. Moreover, it has been shown that the marginal effect of mechanical transmission results in a trend towards faster responses in the vertical as compared to the woven posture, irrespective of task type (Haggard et al., 2006). With regard to the present study, this means that reaction times would be slightly underestimated in the vertical condition and overestimated in the woven condition, assuming the occurrence of any influence at all. Thus, since the direction of a potential effect of mechanical transmission would have been contrary to the hypothesized postural effect on finger processing, it does not require further consideration.

Statistical analysis Trials with reaction times longer than 3000ms[9] were excluded from statistical analysis. This time window was sufficient to respond to the tactile stimuli via the foot pedals, and only 2% of all trials across subjects had to be excluded due to longer reaction times. Furthermore, statistical analysis of reaction times was restricted to correct trials only (88% of valid trials).

To cope with outliers, statistical and descriptive analysis was based on averaged median values, which were calculated for each subject and for every combination of task type and hand posture. As far as possible, error rates were analyzed according to signal detection theory (SDT) and are reported by means of the statistic d'. Due to occasional extreme hit rates of 1, a loglinear transformation (Hautus, 1995) was applied to the data before hit and false-alarm rates were calculated.

[9] This cut-off value is higher than that used in experiment 4 of Haggard et al. (2006), which was set to 2000ms. It accounts for the fact that discriminating between two stimuli requires more time than identifying a single stimulus (Haggard et al., 2006). The cut-off value of 3000ms lies within 2.7 standard deviations above the mean of reaction times. Nevertheless, applying different cut-off values (2000ms and 5000ms) to the data produced the same results.

Statistical analysis was performed with SPSS 16.0, using a linear mixed-effects model. Linear mixed models account for random effects, such as inter-individual differences (West, Welch, & Galecki, 2007). A 2x2 factorial design was applied to the data, with both task type and postural condition constituting single fixed factors.

2.2.2 Results

Results of experiment 1 are presented in Figure 2 and Table 1. Main effects on reaction times of task type ($F_{1,30}$=28.8, p<.001) and posture ($F_{1,30}$=6.2, p=.018) were significant, but the interaction effect of task type and posture ($F_{1,30}$=2.9, p=.096) was not. Nevertheless, it

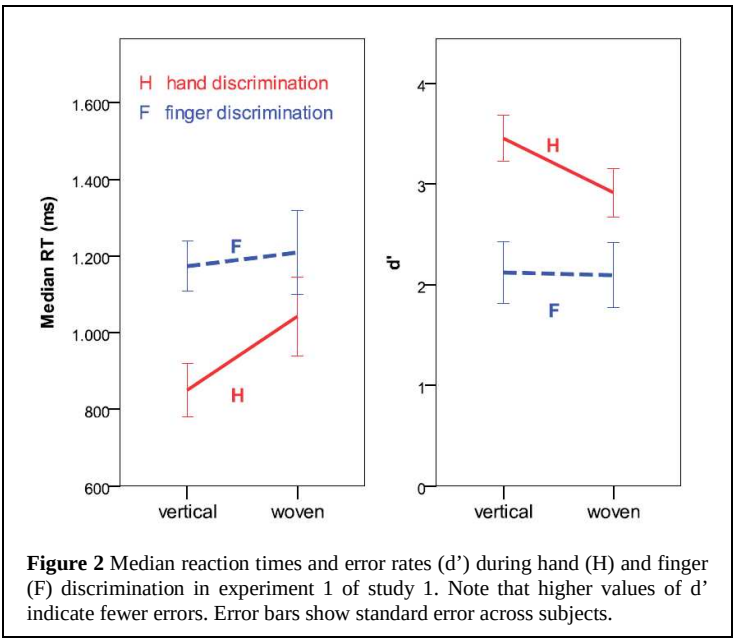

Figure 2 Median reaction times and error rates (d') during hand (H) and finger (F) discrimination in experiment 1 of study 1. Note that higher values of d' indicate fewer errors. Error bars show standard error across subjects.

can be inferred from Table 1 and Figure 2 that the postural effect was almost entirely restricted to the hand discrimination task.

Regarding error rates, only the main effect of task type ($F_{1,30}$=25.9, p<.001) reached statistical significance, while the main effect of posture ($F_{1,30}$=1.8, p=.191) and the interaction of task and posture ($F_{1,30}$=1.5, p=.236) did not. However, error rates show a trend towards the same pattern as was observed for reaction times (Figure 2, note that higher values of d' indicate better performance). The absolute difference in mean d' for hand discrimination was .54 and only .03 for finger discrimination (Table 1).

At the highest level of aggregation the data did not reveal the hypothesized postural effect on finger discrimination. Neither reaction times nor error rates during the finger discrimination task were affected by the postural conditions (Figure 2). A postural influence was found only on hand discrimination. Overall reaction times and error rates were significantly higher in the finger than in the hand discrimination task.

Frequent playing of musical instruments involving precise finger coordination was additionally included as a dichotomic factor in a mixed model analysis. Neither the main, nor any of the interaction effects reached statistical significance. Training in finger coordination had no significant effect on the results.

Table 1 Mean and standard error (SE) across subjects of median reaction times and d' for experiment 1 of study 1.

task	posture	reaction times (ms)		d'	
		mean	SE	mean	SE
hand	vertical	851	69	3.46	.23
hand	woven	1043	103	2.92	.24
finger	vertical	1174	65	2.12	.30
finger	woven	1209	110	2.10	.32

Exploratory analysis Every trial involved the simultaneous stimulation of two fingers. In consideration of four possible stimulation sites, this results in six possible combinations (Figure 3). During each task, two of these combinations served as targets and required a ‘same’ response, while the other four were distractors demanding a ‘different’ response. For example, during hand discrimination, the first two combinations in Figure 3 were targets

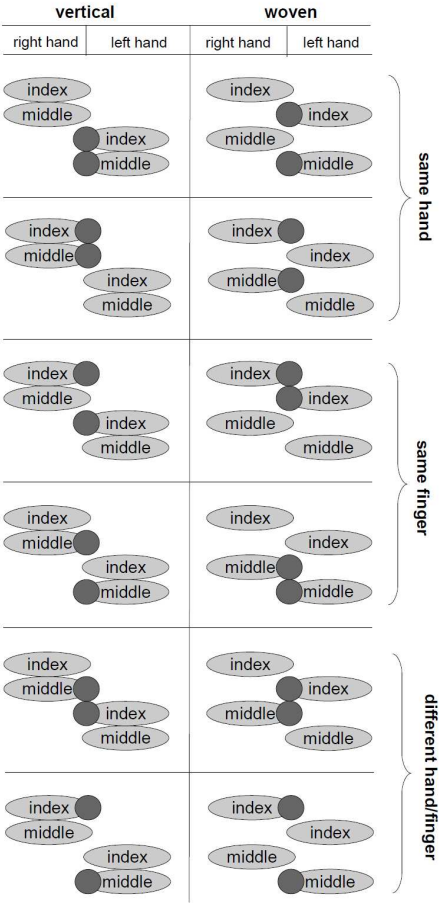

Figure 3 Six possible stimulus combinations (rows) and stimulation categories (curly braces) used in experiment 1 of study 1 during the vertical and the woven posture (columns). Stimulation sites are indicated by circles.

(same hand), while all other combinations were distractors (different hands). The last two combinations in Figure 3 were distractors in both tasks. According to these properties, each pair of associated combinations can be subsumed to a particular stimulation category (Figure 3).

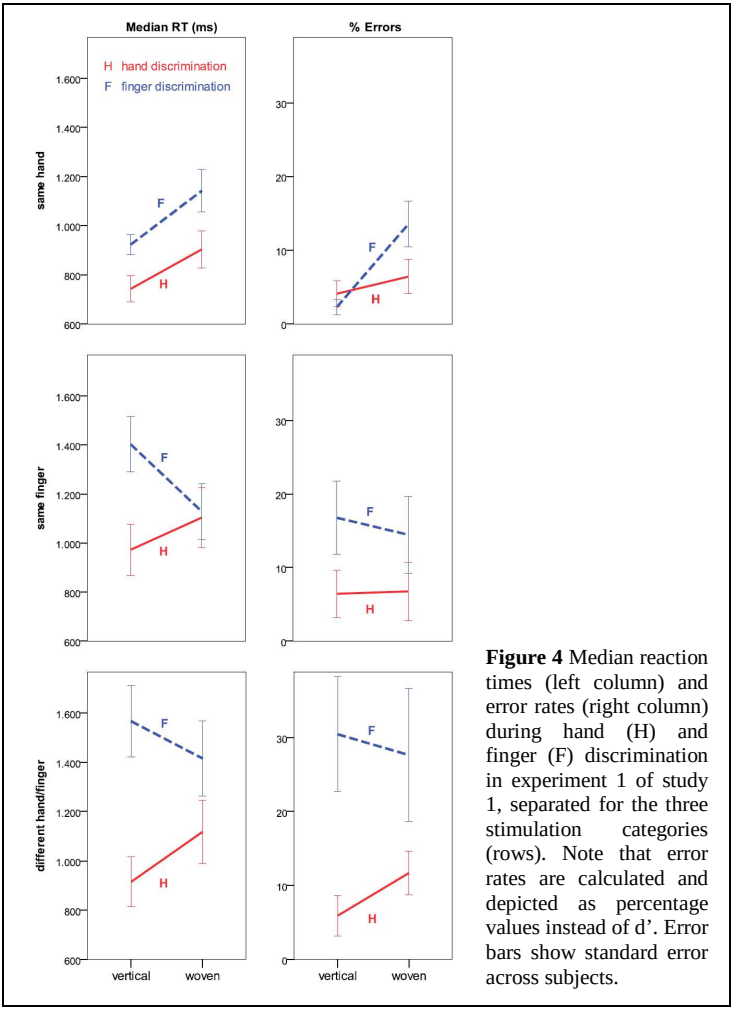

Figure 4 Median reaction times (left column) and error rates (right column) during hand (H) and finger (F) discrimination in experiment 1 of study 1, separated for the three stimulation categories (rows). Note that error rates are calculated and depicted as percentage values instead of d'. Error bars show standard error across subjects.

To account for the fact that these stimulation categories differ from each other in a crucial way (see discussion of experiment 1), the data was analyzed separately for each category.

Figure 4 shows the influence of posture on reaction times and error rates in the hand and the finger discrimination task, separated for the three stimulation categories. At this level of aggregation, error rates could not be calculated according to SDT, as each stimulation category exclusively consists of either targets or distractors with respect to each task and so correct responses are predefined. During finger discrimination, the stimulation category 'same hand' cannot produce true positives, because the stimulus combinations in this category are predefined as distractors. Figure 4 therefore depicts the mean percentages of errors.

In the end, descriptive analysis at this level of aggregation shows that the finger discrimination task was indeed affected by the postural conditions. The direction of this effect, however, varied for the different stimulation categories. Better performance during the woven as compared to the vertical posture was found for the categories 'same finger' and 'different hand/finger', while for the category 'same hand' this pattern was reversed. In contrast, the effect on hand discrimination did not differ between the stimulation categories, constantly resulting in a better performance during the vertical posture. The effect of stimulation category on the direction of the postural effect was entirely restricted to the finger discrimination task.

To ascertain statistical significance for these findings, we analyzed the data separately for the three stimulation categories, focusing on the main effect of posture and its interaction with task type. With respect to reaction times, the main effect of posture reached significance only in the category 'same hand' ($F_{1,30}$=24.3, p<.001) and was not significant in the others (same finger: $F_{1,30}$=1.5, p=.233; different hand/finger: $F_{1,30}$=0.2, p>.5), whereas the interaction effect showed the reversed pattern (same hand: $F_{1,30}$=0.6, p=.45; same finger: $F_{1,30}$=12.0, p=.002; different hand/finger: $F_{1,30}$=7.7, p=.009). This characteristic significance pattern further confirms the conclusion that there is an influence of posture on finger discrimination, the direction of which is modulated by the stimulation categories.

Effects on error rates were statistically not significant, but the trends reflect the pattern obtained for reaction times (Figure 4), thus ruling out the possibility of speed-accuracy trade-offs.

2.2.3 Discussion of Experiment 1

At the highest level of data aggregation, no postural effect on finger discrimination was found. Rearranging the hands from the vertical to the woven posture seems to have no influence on the processing of fingers, neither a facilitating nor an inhibiting one. But this interpretation of our data is too superficial and does not account for the fact that the stimulus combinations used in the discrimination tasks have very distinct characteristics, which are of essential importance concerning their perception. The stimulation categories differ in the degree to which they require finger discrimination to gain a correct answer during the finger discrimination task. The crucial importance of this difference becomes obvious when the following considerations concerning the nature of hand and finger processing are taken into account.

Overall shorter reaction times in the hand discrimination task suggest that the participants are faster in discriminating the hands than they are in discriminating the fingers. Constantly shorter reaction times for hand than for finger identification have also been reported by Haggard et al. (2006). This general advantage for hand processing might reflect the larger familiarity of hand distinction in everyday life. A recent study revealed different processing strategies for tactile stimuli at the fingers of the same vs. different hands (Overvliet, Smeets, & Brenner, 2010). Two stimuli at the same hand are processed in a serial manner, while stimuli applied to different hands are processed in parallel. Therefore, overall shorter reaction times in the hand discrimination task may be explained by the assumption that the process of hand discrimination occurs prior to the processing of fingers, and might even be completed, before finger discrimination starts.

On this basis it seems quite reasonable that a task, which can be solved via hand discrimination alone, will be solved this way, even if

the task description appears to require finger discrimination. Of course, this is true for the hand discrimination task, which, by definition, requires discrimination of the hands. However, also the finger discrimination task, which is supposed to be performed via finger discrimination, can sometimes be solved solely on the basis of hand discrimination: when both tactile stimuli are perceived at the same hand, they must have appeared at different fingers. Only when the stimulus combination involves both hands, discrimination of fingers is inevitable.

This applies to the stimulation categories ‘same finger’ and ‘different hand/finger’ and, as shown in Figure 4, these are exactly the cases in which the finger discrimination task exhibits the postulated advantage in the woven posture. Only the stimulation category ‘same hand’, which can be solved via hand discrimination alone and therefore does not require any finger discrimination, reveals the reversed direction of the postural effect. Characteristically, this is exactly the profile we would expect for the hand discrimination task.

Obviously, the absence of a postural effect on finger discrimination at a higher level of aggregation is caused by the interference of these complementary effects. In contrast, regarding the hand discrimination task, the effect of postural conditions has the same direction in every stimulation category, always producing shorter reaction times and error rates in the vertical posture. Due to the consistency in effect direction, the postural influence on hand discrimination can also be found when all stimulation categories are pooled.

In summary, when finger discrimination was absolutely essential to solve the task and the discrimination of hands provided no information whatsoever about the correct answer, enhanced performance was found in the woven posture. This perceptual advantage for the finger discrimination task when fingers are interwoven is in line with our initial predictions, and demonstrates an influence of body posture on tactile discrimination of fingers.

2.3 Experiment 2

Experiment 2 was conducted in order to support our interpretation of the results from experiment 1, namely that tactile processing of fingers is influenced by a postural representation of the body.

We implemented identification tasks rather than discrimination tasks. Participants were asked to identify the laterality of the touched hand, in the hand identification task, and the type of the touched finger, in the finger identification task, respectively. As in experiment 1, stimulation sites were restricted to the index and middle fingers of both hands. Two tactile stimuli were presented simultaneously to the fingertips of the participants. In the hand identification task, stimulation always involved both fingers of the same hand (i.e., the two stimulus combinations from the category 'same hand'), and in the finger identification task, stimuli always were applied to both fingers of the same type (i.e., stimulus combinations from the category 'same finger') (Figure 3). Both tasks were performed in the vertical and the woven posture (Figure 1a).

The essential difference between the identification tasks implemented here and in Haggard et al. (2006, exp. 4) consists in the fact, that single stimuli were used in the latter, while in the present study both related fingers (as determined by task demands) were touched simultaneously. This implicates an important consequence for the information value of supplemental hand identification during the finger identification task: since in each trial both fingers of the same type were stimulated, supplemental hand identification was not only irrelevant for the correct response, but also did not provide any additional task-irrelevant information concerning the location of the stimuli in peripersonal space.

As in experiment 1 and contrary to the experiments of Haggard et al. (2006), only the index and middle fingers were arranged according to the postural conditions (Figure 1a). Due to this modification, the spatial distance between the four relevant fingers is equal for both postural conditions (see description of experiment 1).

Our hypotheses were exactly the same as in experiment 1. For hand identification, reaction times and error rates should be smaller during the vertical as compared to the woven posture. For the finger

identification task, we expected shorter reaction times and fewer errors during the woven as compared to the vertical posture.

2.3.1 Methods

Participants 16 healthy subjects, five of whom had already taken part in experiment 1, participated in experiment 2. They were recruited from the University of Mannheim and the local community, and were either paid or compensated with course credits. Data from two participants was excluded from further analysis due to extremely slow responses. Mean age of the remaining fourteen participants (7 males) was 24.1, with a range from 20 to 30. According to the Edinburgh Handedness Inventory (Oldfield, 1971), ten were right-handed, three were left-handed and one was ambidextrous. All gave written informed consent previous to the experiment.

As in experiment 1 we assessed past injuries at hands and fingers as well as activities providing frequent exercise regarding finger coordination (e.g., playing musical instruments). These factors had no influence on the results presented here.

Experimental set-up In the finger identification task, denotation of the foot pedals was randomized across subjects. In order to avoid confusion concerning the labels ‘left’ and ‘right’, this randomization was abandoned in the hand identification task. Visual reminders on the occluding screen were changed by the experimenter according to the current task. ‘Left/right’ labels were used for the hand identification task and ‘index/middle’ labels for the finger identification task, respectively. Each block consisted of 30 single trials, so each of the two corresponding stimulus combinations was applied 15 times in randomized order.

All other aspects of the experimental procedure were equal to those of experiment 1.

Statistical analysis The cut-off time for reaction times was set to 2000ms, which seems adequate for identification tasks since only 0.17% of all trials were lost due to longer reaction times, and a cut-

off time of two seconds was also used for motor responses by Haggard et al. (2006, exp. 4). Calculation of reaction times was based on correct trials only (98% of valid trials).

A deviation from the statistical analysis of experiment 1 consists in the calculation of error rates. Again, SDT was applied to the data, but since there is no basis for the classification of the two response alternatives into targets and distractors, the data was analyzed according to a two-alternative forced-choice (2AFC) design, which involves the downward adjustment of d' by a factor of 1/(sqrt 2) (Macmillan & Creelman, 1991).

2.3.2 Results

Again, task type and postural conditions both constituted single factors of a 2x2 factorial design. Means and standard errors (SE) of median reaction times and error rates (d') for each condition are shown in Table 2. Regarding the reaction times, mixed model analysis revealed a strong main effect of task type ($F_{1,39}$=73.5, p<.001), but neither the main effect of posture ($F_{1,39}$=0.9, p=.351) nor the interaction effect of task and posture ($F_{1,39}$=2.6, p=.115) reached a significant level. Since the discrepancy in reaction times between the postural conditions was higher during the hand identification task, and even the trend of a postural effect on finger identification was of the opposite direction (Table 2 and Figure 5), a possible influence on hand identification alone could have been masked by the unaffected finger identification task. To account for this possibility, both tasks were analyzed separately. Supplemental t-tests for paired samples showed a significant effect of posture during the hand identification task (t_{13}=-2.8, p=.008, one-tailed), while no differences in reaction times could be observed for the finger identification task (t_{13}=0.4, p=.333, one-tailed).

Table 2 Mean and standard error (SE) across subjects of median reaction times and d' for experiment 2 of study 1.

task	posture	reaction times (ms)		d'	
		mean	SE	mean	SE
hand	vertical	362	14	2.63	.03
hand	woven	393	19	2.55	.05
finger	vertical	486	26	2.20	.08
finger	woven	478	25	2.40	.09

The analysis of error rates revealed a different pattern of results (Figure 5). Again, there was a significant main effect of task type ($F_{1,39}$=23.0, p<.001), whereas the main effect of posture remained non-significant ($F_{1,39}$=0.9, p=.359). The interaction effect of task

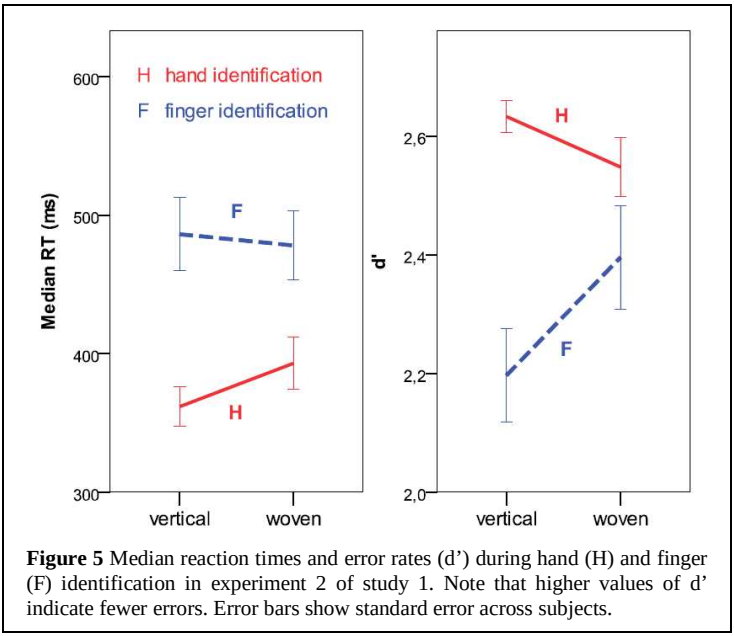

Figure 5 Median reaction times and error rates (d') during hand (H) and finger (F) identification in experiment 2 of study 1. Note that higher values of d' indicate fewer errors. Error bars show standard error across subjects.

type and posture ($F_{1,39}$=5.3, p=.026) reached significance as well, indicating a different effect of posture on both tasks. When analyzed separately for each task using paired t-tests, significant differences between the postural conditions could only be confirmed for the finger identification task (t_{13}=-2.1, p=.029, one-tailed), but not for the hand identification task (t_{13}=1.4, p=.092, one-tailed). However, it should be pointed out here that in the hand identification task, errors were extremely rare (less than 1% of all trials), which could have concealed an effect of posture.

2.3.3 Discussion of Experiment 2

Experiment 2 was conducted to confirm the hypothesis that finger identification depends on a postural representation of the fingers, as it has already been shown for the hands. By stimulating both fingers of the same type rather than just one, we tried to suppress implicit hand processing during the finger identification task. Since every trial involves the stimulation of both hands, supplemental processing of the associated hand provides no incremental information about the location of the stimuli in peripersonal space.

We focused on two different performance measures, namely reaction times and error rates. In the finger identification task, postural conditions had no effect on reaction times, while significantly fewer errors were observed during the woven as compared to the vertical posture. Thus, the hypothesis of faster responses during the woven posture was disproved by the data, but the assumption of fewer errors during the same condition was confirmed. In the hand identification task, the reversed pattern was observed: while the participants did respond to the stimuli significantly faster during the vertical condition, error rates were equal for both postures.

Both reaction times and error rates are equally important regarding performance, because they are directly related to each other. In speed tasks, fewer errors within the same time are comparable to faster responses accompanied by the same number of

errors. Experiment 2, therefore, confirms our initial assumption of a postural influence on both hand and finger identification.

A direct comparison with the results of Haggard et al. (2006) revealed another interesting detail: while the overall reaction times, aggregated over the postural conditions, during hand identification are approximately equal in both studies (377 ms here and about 370 ms in Haggard et al., 2006, exp. 4), there is a considerable difference in the overall reaction times during finger identification (482 ms here vs. about 700 ms). Thus, the differences between the identification tasks implemented in the two studies seem to selectively affect overall reaction times in the finger identification task. Apparently, this task can be solved faster when both fingers of a respective type are stimulated simultaneously. This supports our initial assumption that the finger identification task, as it was implemented by Haggard et al. (2006), implicitly involved supplemental hand processing. In our version of the task, supplemental hand identification was ineffectual to localize the stimuli in peripersonal space. Therefore, it was omitted, which in turn led to faster responses.

The possibility that shorter reaction times during the finger identification task in the present experiment were solely caused by the acceptance of more errors is disproved by the fact that the present implementation of the identification tasks even produced fewer errors.

2.4 Discussion

The aim of the present study was to provide evidence for the tactile processing of body parts within a spatial frame of reference. Based on considerations about the mental segmentation of peripersonal space, we expected hand and finger processing to be conversely affected by two postural conditions. In the vertical posture, index finger and middle finger of the right hand were placed above those of the left hand, and in the woven posture, index and middle fingers of both hands were interleaved (Figure 1a). Hand processing should be facilitated during the vertical and finger processing during the woven posture.

These hypotheses conflict with the results of Haggard et al. (2006), who applied single tactile stimuli to the fingertips of their participants and asked them to identify the touched hand or the touched finger type, respectively, during a vertical and a woven posture. A perceptual advantage for hand identification during the vertical posture was found, but finger identification was unaffected by the postural conditions. The authors' interpretation was that fingers cannot be processed within an external frame of reference.

However, this interpretation does not account for the differential information value of hand and finger processing (see Introduction). Mere finger identification is insufficient in order to localize a single tactile stimulus within an external frame of reference, because its location might differ highly, depending on the laterality of the stimulated hand. When touched at a specific finger, humans might automatically process the laterality of the associated hand, even when it is irrelevant for the correct response. These considerations suggest an alternative explanation of the results: the finger identification task, as it was implemented by Haggard et al. (2006), might have elicited an implicit processing of the laterality of the associated hand. This would confound two processes, namely finger and hand identification, which we assume to be conversely affected by the postural conditions. Thus, a postural effect on the finger identification task might have been concealed by the overlap of two opposed effects.

To investigate the processing of fingers within an external frame of reference, it is of fundamental importance to implement a finger task which is unlikely to cause an implicit processing of the hands. However, the task's theoretical independence of hand laterality is not sufficient for this purpose. It must rather be reliably ruled out that supplemental hand processing could be of any informative value concerning the location of the stimulated finger.

In experiment 1, this was achieved by implementing discrimination tasks rather than identification tasks. Supplemental hand processing during the finger discrimination task provided no incremental spatial information, since targets involved the stimulation of both hands anyway. In experiment 2, we implemented identification tasks and eliminated supplemental hand processing during the finger task by simultaneously stimulating both fingers of the same type. As every trial involved the stimulation of both hands, identification of the associated hands became entirely meaningless

and provided no spatial information at all. Substantially higher reaction times were found for the discrimination tasks as compared to the identification tasks (see Table 1 and 2), suggesting different underlying mechanisms (Haggard et al., 2006). However, these are irrelevant for the conclusions drawn here, since the purpose of study 1 was not to investigate the underlying mechanisms of discrimination and identification tasks, but postural effects on hand and finger processing within these tasks.

Separate analysis of the stimulation categories in experiment 1 revealed a strong postural influence on finger discrimination, with faster responses during the woven posture. Only when hand discrimination alone provided enough information for reliable judgements, the influence of the postural conditions was reversed, favoring the vertical posture. The same postural influence was found for the finger identification task in experiment 2, where participants made fewer errors when their fingers were interleaved. Compared to the results by Haggard et al. (2006), overall reaction times were reduced selectively during finger identification, confirming assumption that an additional process occurred when only one finger was stimulated. Regarding hand processing, a perceptual advantage of the vertical posture was found in both experiments, indicating the basic coherence to the study of Haggard et al. (2006).

Taken together, our results are incompatible with the assumption of a mere somatotopic representation of the fingers. Influences of body posture on finger discrimination and finger identification have consistently been found in the experiments described here. As it has been shown for the hands (Haggard et al., 2006; Schicke & Röder, 2006; Shenton, Schwoebel, & Coslett, 2004; Shore et al., 2002), processing of the fingers is modulated by their posture in peripersonal space.

In both experiments of study 1, a perceptual advantage for finger processing was found during the woven posture, while hand processing was facilitated during the vertical posture. These directions of the postural effects are consistent with our initial predictions based on considerations about the mental segmentation of peripersonal space. Generally speaking, performance always was enhanced when the fingers were grouped according to the relevant dimension, i.e., laterality of the associated hand in the hand tasks and finger type in the finger tasks. In accordance with our results, we

propose that the spatial distance between related and unrelated fingers (as determined by task requirements) constitutes the basis for a mental segmentation of peripersonal space into task-relevant subdivisions. This segmentation of peripersonal space facilitates the association between tactile stimuli, localized within external coordinates, and specific body parts, currently occupying the same spatial area. Assigning a tactile stimulus to the touched body part (within an external reference system) only requires the distinction of discrete spatial areas and the localization of the stimulus within one of these areas. In a given task, each of these spatial fields is associated with a specific response. Therefore we will refer to them as response fields, which we define as task-relevant subdivisions of peripersonal space, representing a specific response alternative.

If semantically linked response fields, i.e., representing the same response alternative, are spatially close to each other and not separated by response fields representing a different response alternative, they can be considered as being grouped, according to general grouping principles like proximity and shared features. Gestalt principles within the somatosensory domain (Gallace & Spence, 2011; Serino, Giovagnoli, de Vignemont, & Haggard, 2008).

The configuration of response fields depends on body posture and task requirements. These factors were systematically manipulated in the present study. With respect to the hand tasks, related fingers were grouped during the vertical posture, thereby constituting two relatively large response fields. In the woven posture, each response alternative (i.e., each hand) was represented by two smaller response fields rather than a single one. For the finger tasks, this relation was reversed, because here it was the woven posture in which each response alternative was represented by one single response field, whereas the vertical posture revealed two response fields for each response alternative (Figure 1b).

We assume that cognitive load increases with the number of response fields that have to be attended to simultaneously and with the degree to which different response fields are distinguishable from each other. Well discriminable response fields should be large, spatially distant and of limited number.

Throughout study 1, the directions of the postural effects on both the hand and the finger tasks were in accordance with the conceptualization of response fields. In both experiments, we found a perceptual advantage for hand processing during the vertical

posture and for finger processing during the woven posture. The mental segmentation of peripersonal space into response fields seems to be a basic principle for the assignment of tactile stimuli to body parts within an external frame of reference. The configuration of response fields and its dependency on experimental variations of body posture and task requirements should be considered in future investigations on tactile processing of body parts within an external reference system.

3 Study 2: Testing Response Fields in Peripersonal Space

The results of study 1 suggested that tactile identification of body parts within an external frame of reference depends on an association between the external coordinates of tactile stimuli and spatially related body parts. Dynamic qualities of spatial representations suggest that this association might be strengthened by a mental segmentation of peripersonal space into response fields, depending on a postural representation of the body.

In three experiments we investigated the influence of size, number and relative distance between response fields on tactile hand identification. Healthy subjects received single tactile stimuli at their fingertips and were asked for speeded responses regarding the laterality of the stimulated hand. The task was performed under different hand postures, modulating the number, the size and the distance between response fields. The results show that reaction times are affected by the spatial distance between response fields (experiment 1), but not by their number and size (experiment 2 and 3). Based on these results, a modification of the concept of response fields is proposed.

3.1 Introduction

Tactile stimuli are localized within an external frame of reference (Azañón & Soto-Faraco, 2008; Head & Holmes, 1911; Heed, Backhaus, & Röder, 2012). The localization of touch within external spatial coordinates allows for rapid movements towards the origin of a tactile stimulus, e.g., a mosquito bite (Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995). It has been shown that this automatically driven process affects the identification of stimulated body parts (study 1 of this thesis and Haggard et al.,

2006). Although the determination of a touched body part can be solved on the basis of a somatotopic reference system (Penfield & Rasmussen, 1950), body posture has a significant impact on performance. In several studies, in which tactile stimuli were delivered to the fingertips, identification of hand laterality was impaired when the fingers of both hands were interleaved, compared to when both hands were separated in space (study 1 of this thesis, Haggard et al., 2006.; Zampini et al., 2005).

A prerequisite for an external reference system consists in a representation of external space, which emerges from integrated multisensory information (Graziano & Gross, 1998; Holmes & Spence, 2004; Làdavas et al., 1998; Làdavas & Farnè, 2004). Especially peripersonal space, i.e., the space within reaching distance, is pertinent for an adequate interaction within the environment. Stimuli within reaching distance are processed differently than stimuli outside this spatial region (Iriki et al., 1996; Longo & Lourenco, 2006).

The representation of peripersonal space is not static, but exhibits dynamic qualities (Holmes & Spence, 2004; Legrand et al., 2007; Làdavas & Farnè, 2004). In several studies it has been shown that manipulations of the reaching distance by using tools are capable of extending peripersonal space. Remote areas, previously represented as extrapersonal space (i.e., out of reach), became immediately relevant for potential actions, and thus were integrated in the representation of peripersonal space (Longo & Lourenco, 2006; Longo & Lourenco, 2007; Làdavas & Farnè, 2004). The converse effect, a contraction of peripersonal space, has also been reported (Lourenco & Longo, 2009). Evidence for the plasticity of spatial represention stems from electrophysiological studies with macaque monkeys (Iriki et al., 1996; Maravita & Iriki, 2004) and from behavioral studies with human subjects (Maravita et al., 2002; Yamamoto & Kitazawa, 2001).

Not only are the boundaries of peripersonal space dynamic, but also the relative resolution of its parts. Some areas within peripersonal space are overrepresented with respect to others (Driver & Grossenbacher, 1996; Lloyd, 2007; Làdavas et al., 1998; Reed et al., 2006; Reed et al., 2010; Short & Ward, 2009; Whiteley et al., 2008). For example, Reed et al. (2006) reported shorter reaction times to visual stimuli presented close to the hands than to the same stimuli presented further away from the hands (but still within

reaching distance). This finding was interpreted in terms of spatial attention. Areas directly surrounding the hands are more relevant for immediate actions than distant areas. In a recent study, even a difference between the space near the palm of the hand (relevant for immediate grabbing) and the back of the hand (relatively irrelevant) could be verified (Reed et al., 2010). Importantly, these dynamics in spatial representations occurred also when only proprioceptive information of the hand position was available, i.e., when the hand was hidden from view (Makin et al., 2007; Reed et al., 2006).

Within an external frame of reference, tactile sensations are processed according to their external spatial coordinates, and the body parts currently occupying that space are identified within the same reference system (Azañón & Soto-Faraco, 2008; Holmes & Spence, 2004; Kitazawa, 2002; Shore et al., 2005). The dynamic qualities of the representation of peripersonal space form the basis for a potential mechanism to strengthen this association between the external coordinates of tactile stimuli and the spatially related body parts. For example, the tactile identification of hands is facilitated by a mental segmentation of peripersonal space into two distinct areas, each of which is occupied by one hand. In this situation, hand identification only requires the localization of the stimuli within one of these discrete spatial areas, rather than a supplemental assignment of the spatial area to the related hand. Based on these considerations, the concept of response fields was proposed in study 1. Response fields were defined as ‘task-relevant subdivisions of peripersonal space, representing a specific response alternative’ (see Discussion of study 1).

The segmentation of peripersonal space into response fields depends both on task demands and body posture. When the task requires a distinction between the hands, the configuration and the number of response fields should differ depending on hand posture. An example for the ‘vertical’ and the ‘woven’ posture, which were used in study 1 and in Haggard et al. (2006) is illustrated in Figure 1. In the vertical posture, fingers are grouped according to the associated hand, and therefore all parts of each hand can be represented by a single response field. In the woven posture, however, the fingers of both hands are interleaved and peripersonal space cannot be segmented into two discrete spatial areas distinctively representing all parts of one hand. According to the previous conceptualization specified in study 1, in the woven posture

each response field is split into two smaller ones, which are separated by a response field representing the other hand (Figure 1).

In study 1, participants received light tactile stimuli at the fingertips, while they were holding their hands in either the vertical or the woven posture, and they were asked to identify the laterality of the touched hand. Consistent with the conceptualization of response fields, a better performance for hand identification was found during the vertical as compared to the woven posture. Furthermore, when the participants were asked to identify the type of the touched finger (i.e., index or middle) and hand laterality was completely irrelevant, a perceptual advantage for the woven posture appeared (Figure 5). This finding is also in line with the conceptualization of response fields, because it is the woven posture, in which the fingers are grouped according to finger type, thereby allowing for the formation of two (rather than four) response fields (Figure 1b).

A mental segmentation of peripersonal space into response fields would enhance the association between spatial areas and specific body parts, and an increase in the number of response fields that have to be attended to simultaneously therefore should increase the cognitive load and result in lower performance. Furthermore, the differentiation of response fields might be influenced by their size and their relative distance from each other. According to the previous conceptualization of response fields, well-discriminable response fields should be large, spatially distant and of limited number (see Discussion of study 1).

The aim of study 2 was to investigate the impact of these three factors on the discriminability of response fields and to provide further evidence for the practicability of the concept in the scope of tactile perception within an external reference system.

Three experiments on tactile hand identification were conducted, in which the relative distance, the number and the size of response fields were systematically varied. In all three experiments, tactile stimuli were applied to the fingertips and participants were asked to indicate the laterality of the stimulated hand. In experiment 1, the spatial distance between the hands was manipulated. Experiments 2 and 3 focused on the influence of the number and the size of the response fields for each hand.

3.2 Experiment 1

Experiment 1 was conducted to test the influence of spatial distance between response fields on the tactile identification of hand laterality. Single tactile stimuli were applied to the tips of index and middle fingers of both hands, while the participants arranged their hands according to one of two postural conditions. In the adjacent posture, the index and middle fingers of one hand were placed directly above the same fingers of the other hand. In the separated posture, the fingers of the upper hand were lifted vertically by 10 cm (Figure 6a). Participants were asked for speeded responses regarding the laterality of the touched hand. According to the concept of response fields and its postulated dependency on spatial distance, we expected shorter reaction times during the separated as compared to the adjacent posture.

The middle finger of the upper hand and the index finger of the lower hand (in the following referred to as interior fingers) were closer to the respective other hand than it is the case for the middle finger of the lower hand and the index finger of the upper hand (referred to as exterior fingers) (Figure 6a). The spatial proximity to a conflictive response field should impair the allocation of the stimuli within the correct response field. We therefore hypothesized higher reaction times after stimulation of the interior fingers than after stimulation of the exterior fingers. Furthermore, the effect of relative finger position (stimulation of interior vs. exterior fingers) was expected to be more pronounced in the adjacent as compared to the separated posture.

3.2.1 Methods

Participants 19 healthy participants were recruited from the University of Mannheim and the local community. They were either paid or received course credit. The data of two participants were excluded from analysis because of extremely slow responses (reaction times were three standard deviations above the mean) and

dysfunctions of the technical set-up. Mean age of the remaining 17 participants (7 males) was 26.6 years, and all but two were right-handed (Oldfield, 1971). All participants gave written informed consent previous to the experiment.

Experimental and statistical procedures Participants were seated comfortably at a desk, deprived from the view of their hands. Index and middle fingers of both hands were arranged according to the two postural conditions (see Figure 6a). The other fingers and the thumbs were held at the ipsilateral side. Contact between the hands was prevented. To ensure the comparability of hand posture between different subjects, a wooden framework with two horizontal sticks, separated by 10cm, was fixed on the desk. In the adjacent posture, participants held the fingers of one hand below and the fingers of the other hand above the lower stick. In the separated posture, the fingers of one hand were placed below the lower stick and the fingers of the other hand on top of the upper stick. The postural conditions are depicted in Figure 6a. Thus, the spatial distance between the stimulated fingers of both hands was exactly 4mm in the adjacent and 10cm in the separated posture. Direct skin contact between fingers of different hands was prevented in order to eliminate mechanical transmission of the stimuli. The vertical positions of the hands were randomized across participants.

Tactile stimuli were delivered via miniature solenoids (RS Components, model 330-5213) that were attached to the fingertips with adhesive tape. A well-noticeable tactile sensation was induced by a pulse length of 20ms. During the experiment, participants wore active noise-cancelling headphones (Audio Technica ATH-ANC7, QuietPoint®), in order to reduce acoustic disturbance caused by the solenoids. Responses were given with foot pedals in a congruent manner, i.e., touches at the right hand were indicated by pressing the right pedal and touches at the left hand by pressing the left pedal.

The sequence of the postural conditions was randomized across subjects. In both conditions, each of the four relevant fingers was stimulated ten times in randomized order. The intertrial interval varied randomly between three and five seconds. Stimulus sequences were controlled using Presentation v14.2 (Neurobehavioral Systems, Inc., CA, USA). Participants were urged to respond as fast as possible.

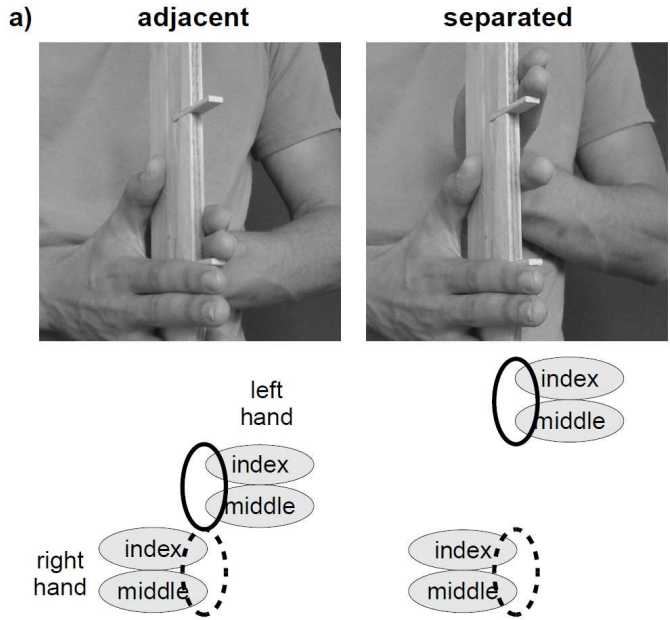

Figure 6 a) Postural conditions and corresponding response fields for experiment 1 of study 2. Dotted circles indicate response fields for the right hand. **b)** Results from experiment 1. Error bars show standard error across subjects.

Due to extremely few errors (0.4%), error rates were not statistically analyzed. Nevertheless, it was assured that speed-accuracy tradeoffs can impossibly account for the results, because more errors concurred with higher reaction times. Erroneous trials and responses given later than two seconds after stimulation were discarded. Statistical analysis was based on median reaction times.

Data were analyzed in R (Version 2.13.1).

3.2.2 Results

Results are presented in Figure 6b and Table 3. The data were analyzed according to a linear mixed-effects model including the factors posture (adjacent vs. separated) and relative finger position (interior vs. exterior fingers). Participants were specified as random factor. The main effect of posture ($F_{1,48}$=8.36, p<.01) was significant, indicating that reaction times were shorter during the separated as compared to the adjacent posture (Figure 6b). Neither the main effect of relative finger position ($F_{1,48}$=0.3, p>.5) nor the interaction between both factors ($F_{1,48}$=2.22, p=.14) reached a significant level.

The effect of relative finger position was expected to be more pronounced during the adjacent posture, a hypothesis which is further confirmed by the interactive trend in the mixed model analysis. Therefore, the effect of relative finger position was analyzed separately for both postural conditions. One-tailed t-tests for paired samples showed a significant effect of relative finger position during the adjacent posture (t_{16}=2.54, p=.01) and no such effect during the separated posture (t_{16} =-1.11, p=.86). Thus, when the stimuli appeared spatially close to the conflictive response field (i.e., representing the other response alternative), reaction times increased significantly.

Table 3 Mean and standard error (SE) across subjects of median reaction times for experiment 1 of study 2.

posture	finger position	reaction times (ms)	
		mean	SE
adjacent	interior	406	15
adjacent	exterior	397	16
separated	interior	386	14
separated	exterior	390	13

3.2.3 Discussion of Experiment 1

Experiment 1 clearly shows that reaction times in a simple hand identification task are dependent on the spatial distance between the stimulated fingers. In the separated posture, when fingers of different hands were separated by 10cm, reaction times were significantly shorter than in the adjacent posture, when fingers of different hands were adjacent (Figure 6a). The spatial distance between the fingers of the right and those of the left hand facilitated the distinction between the two corresponding response fields.

This result extends previous findings of attentional interferences between task-relevant and task-irrelevant tactile stimuli (Driver & Grossenbacher, 1996; Pavani et al., 2000; Soto-Faraco et al., 2004). For example, Driver & Grossenbacher (1996) asked their participants to discriminate between two qualitatively different tactile stimuli applied to their right hand, while ignoring similar stimuli presented simultaneously to their left hand. Task-irrelevant and task-relevant stimuli were either congruent or incongruent. The effect of congruency (i.e., decreased performance for incongruent trials) was enhanced, when the irrelevant stimuli appeared spatially close to the attended stimuli (Driver & Grossenbacher, 1996). Many studies confirmed that the congruency effect depends on the distance of the stimuli in external space and not on the somatotopic distance of the stimulated body parts (Gallace, Soto-Faraco, Dalton, Kreukniet, & Spence, 2008; Pavani et al., 2000; Soto-Faraco et al., 2004).

Furthermore, we found higher reaction times when the stimuli appeared adjacent to the response field representing the conflictive response. This effect was only found for the adjacent posture, because in the separated posture, no finger was adjacent to the conflictive response field and the spatial distance was at least 10cm (Figure 6a). This result particularly confirms the idea of response fields in peripersonal space, for the decreased performance after stimulation of the interior fingers can only be caused by the spatial pattern of the tactile stimuli. Neither the type of interior fingers (which was randomized) nor mechanical transmission of the stimuli from the touched finger to the other hand (which was eliminated) can account for the increase in reaction times.

Overall, the results of experiment 1 show that (i) the spatial distance between the hands facilitates tactile hand identification and that (ii) the assignment of a tactile stimulus to the touched hand is impaired by the spatial proximity to the other hand. These results are consistent with the concept of response fields, which were characterized as alleviating tactile processing within an external reference system, when they are spatially distant from each other.

3.3 Experiment 2

In experiment 2 we investigated whether reaction times in a hand identification task are affected by the number and size of response fields, which are associated with a specific response alternative. As in experiment 1, single tactile stimuli were delivered to the tips of the index and middle fingers of both hands, and participants were asked to indicate the laterality of the touched hand as quickly as possible. The task was conducted under two postural conditions. In the right-enclosed posture, the right fingers were adjacent, only separated by a wooden stick (4mm) and surrounded by the fingers of the left hand. In the left-enclosed posture, this configuration was reversed: the left fingers were adjacent and surrounded by the right fingers. The postural conditions are depicted in Figure 7a.

The previous conceptualization of response fields based on the results of study 1 involves the assumption that one response field,

representing a specific response alternative, can be split up into two smaller ones, when these are separated by another response field, representing a different response alternative (an example is illustrated in Figure 1b). According to this assumption, the number and size of response fields for the right and the left hand should differ depending on the postural conditions. The right hand is represented by one large response field in the right-enclosed posture and by two small response fields in the left-enclosed posture. This configuration is reversed for the left hand. We hypothesized that reaction times following the stimulation of the right hand are shorter in the right-enclosed as compared to the left-enclosed posture. In contrast, reaction times to stimuli at the left hand were expected to be shorter in the left-enclosed as compared to the right-enclosed posture.

3.3.1 Methods

Participants Experiment 2 was conducted subsequently to experiment 1, and performed by the same group of participants. All gave written informed consent.

Experimental and statistical procedures In both postural conditions, the interior fingers were separated by the lower stick of the wooden framework described in experiment 1. In this vein, mechanical transmission between fingers of the same hand was eliminated. Apart from the postural conditions, the experimental set-up was the same as in experiment 1. All technical details and procedures are described in the method section of experiment 1.

Error rates were extremely low (0.8%) and not statistically analyzed.

Table 4 Mean and standard error (SE) across subjects of median reaction times for experiment 2 of study 2.

touched hand	posture	reaction times (ms)	
		mean	SE
right	right-enclosed	431	17
right	left-enclosed	443	18
left	right-enclosed	442	12
left	left-enclosed	447	16

3.3.2 Results

Results are shown in Figure 7b and Table 4. The data were analyzed with a linear mixed effects model (2x2 factorial design). The two factors were constituted by the laterality of the stimulated hand and the two postural conditions. Subjects were included as random factor. According to our hypothesis, the interaction between the stimulated hand and the postural conditions was of major interest. However, no interaction between these factors was found ($F_{1,48}$=0.13, p>.5). Neither the main effect of posture ($F_{1,48}$=0.85, p=.36) nor the main effect of stimulated hand ($F_{1,48}$=0.6, p=.44) were statistically significant.

When analyzed separately using paired t-tests, no significant effects were found for the right hand (t_{16}=1.04, p=.16) and for the left hand (t_{16}=-0.35, p>.5). Regarding the detection of the left hand, marginal effects were even directed contrary to our hypotheses (Figure 7b).

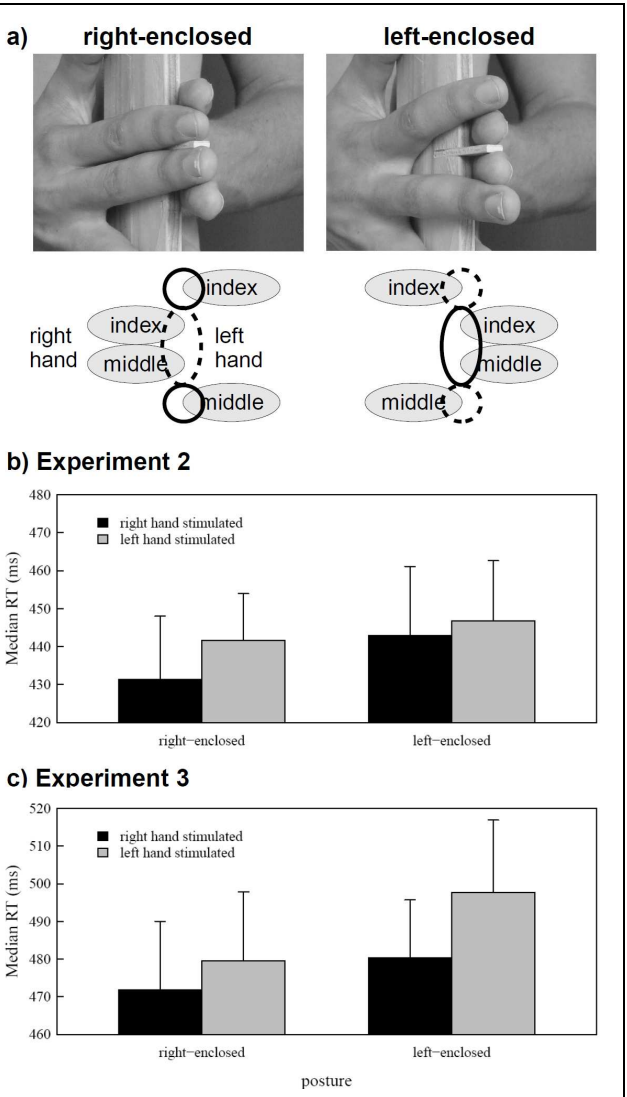

Figure 7 a) Postural conditions and corresponding response fields for experiment 2 and 3 of study 2, according to the previous conceptualization of response fields. Dotted circles indicate response fields for the right hand. **b)** Results from experiment 2 and **c)** experiment 3. Error bars show standard error across subjects.

3.3.3 Discussion of Experiment 2

In experiment 2, we expected shorter reaction times when both fingers of the stimulated hand were adjacent rather than separated by fingers belonging to the other hand, as it was the case in the right-enclosed posture for the right and in the left-enclosed posture for the left hand (Figure 7a). This hypothesis was drawn from the assumption that the number and size of response fields for each hand is modulated by these postural conditions. However, the results did not reveal any effects of posture, and a modulating influence of the number or the size of response fields on reaction times could not be confirmed. During both postures and with respect to both hands, reaction times were approximately equal and did not differ substantially. Contrary to our hypotheses, reaction times after stimulation of the left hand were even higher in the left-enclosed as compared to the right-enclosed posture. In experiment 2, no influence of number and size of response fields on the performance in the hand identification task could be verified.

However, retrospective considerations indicated that the absence of postural effects might as well be accounted for by the design of the implemented task. Participants were instructed to react to the stimulation of both the right and the left hand. This was possible only when the participants' attention was divided between the response fields of the right and those of the left hand, because the stimuli could occur within both (the order of stimulation was randomized). As a consequence, there were always three response fields, which had to be attended simultaneously, regardless of the postural condition. Although the meaning of the response fields changed with posture, their total number and size remained constant. This possible explanation for the absence of postural effects in experiment 2 was specifically tested in experiment 3.

3.4 Experiment 3

To ensure that attending the response fields of only one hand was sufficient to solve the identification tasks, participants in experiment 3 reacted only to stimuli at one specific hand. Single tactile stimuli were applied to the index and middle fingers of both hands, which were held either in the right-enclosed or in the left-enclosed posture (Figure 7a). An additional factor was constituted by the attended hand. In the right hand task, participants were instructed to react only to stimuli at their right hand and to ignore those at their left hand, and vice versa in the left hand task. Due to this modification of experiment 2, attended response fields differed between the postural conditions, depending on the laterality of the attended hand. For the right hand task, the right-enclosed posture should result in one large response field and the left-enclosed posture in two small ones. For the left hand task, this configuration should be reversed. It was hypothesized that reaction times in the right hand task were shorter in the right-enclosed as compared to the left-enclosed posture. For the left hand task, shorter reaction times were expected in the left-enclosed as compared to the right-enclosed posture.

3.4.1 Methods

Participants 19 healthy students (8 males, mean age was 25.3 years) from the University of Mannheim, seven of which also took part in experiment 1 and 2, participated in experiment 3. All but three were right-handed and one was ambidextrous (Oldfield, 1971). All gave written informed consent to the experiment.

Experimental and statistical procedures The order of tasks (i.e., whether the right or the left hand should be attended) was randomized across subjects. To reduce confusion concerning the instructions, the order of the postural conditions was randomized only within the tasks. Speeded responses were given with the foot ipsilateral to the attended hand.

The experimental set-up was the same as in experiment 1 and 2. The postural conditions are described in experiment 2 and in Figure 7a and all technical details and procedures in the method section of experiment 1.

3.4.2 Results

Results are shown in Figure 7c and Table 5. Data were analyzed with a linear mixed effects model (2x2 factorial design), containing the factors attended hand and postural condition. Neither the interaction effect ($F_{1,54}$=0.24, p>.5), which was of major interest, nor one of the main effects (attended hand: $F_{1,54}$=1.63, p=.21; posture: $F_{1,54}$=1.85, p=.18) reached a significant level. Separate t-tests revealed no significant effect for the right hand (t_{18}=0.78, p=.22) and neither for the left hand (t_{18}=-1.14, p>.5).

During both postural conditions, stimulation of the right hand resulted in slightly shorter reaction times than stimulation of the left hand (Figure 7c), a trend that has also been found in experiment 2 (Figure 7b). This marginal difference can be explained by faster reactions to stimuli at the dominant hand (and with the dominant foot), since most participants in experiment 2 and 3 were right-handed.

Table 5 Mean and standard error (SE) across subjects of median reaction times for experiment 3 of study 2.

attended hand	posture	reaction times (ms)	
		mean	SE
right	right-enclosed	472	18
right	left-enclosed	480	15
left	right-enclosed	480	18
left	left-enclosed	498	19

3.4.3 Discussion of Experiment 3

Experiment 3 was designed to eliminate the need for divided attention between both hands, a factor that might have concealed an influence of the postural conditions in experiment 2. In the right-enclosed posture, there was supposed to be one large response field for the right hand and two small ones for the left hand, and vice versa in the left-enclosed posture. Consequently, when the participants' attention is divided between both hands, three response fields would have to be attended, regardless of the postural conditions. In experiment 3, participants were instructed to react only to stimuli at one specific hand and to ignore those occurring at the other hand. Due to this modification, only the response fields for one hand would have to be attended, rather than the sum of response fields for both hands.

Despite this modulation, experiment 3 revealed the same results as were obtained in experiment 2. No influence of the postural conditions on reaction times was found, neither regarding identification of the right hand nor identification of the left hand. An effect of the number and the size of response fields on reaction times in hand identification could not be verified, even when the participants' attention was directed to one specific hand. In spite of null findings, these results absolutely disqualify the initial assumption that reaction times are affected by the size and the number of response fields, because not even a non-significant interaction effect in the expected direction was found. This result has important implications on the conceptualization of response fields and will be discussed in the next section.

3.5 Discussion

The present study was devoted to the dynamic qualities of the representation of peripersonal space and their influence on tactile identification of body parts. Specifically, we investigated the characteristics of response fields, which were defined as task-

relevant subdivisions of peripersonal space, each representing a specific response alternative within a given task (study 1). Using an external reference system, a mental segmentation of peripersonal space into discrete spatial areas should facilitate the tactile identification of touched body parts, because it only requires the localization of tactile stimuli within one of these areas and an association of that area with a specific response. This mental segmentation of peripersonal space is enabled by the dynamic qualities of spatial representations (Holmes & Spence, 2004; Legrand et al., 2007; Longo & Lourenco, 2006; Reed et al., 2006; Reed et al., 2010). According to a previous conceptualization based on the results of study 1, response fields should be large, spatially distant and of limited number, to be maximally distinguishable from each other (see Discussion of study 1).

In order to test the impact of these three factors on the tactile identification of body parts, three experiments were conducted. Each experiment consisted in a simple hand identification task, which was performed under different postural conditions. Single tactile stimuli were delivered to the index and middle fingers of both hands, and the participants were asked for speeded responses about the laterality of the touched hand. Experiment 1 was designed to investigate the influence of spatial distance between response fields (Figure 6). In experiment 2 and 3, the postural conditions were selected in order to manipulate the number and size of response fields (Figure 7).

The results of experiment 1 show that reaction times in a simple hand identification task depend on the spatial distance between the external coordinates of the stimuli and the untouched hand. When the distance between hands is large, stimuli can be faster assigned to the associated hand. In contrast, when the untouched hand is spatially close to the location of the tactile stimulus, increased reaction times have been found. Importantly, this effect is not only mediated by the mere distance between the hands, but rather by the distance between the tactile stimuli and the hand, which had not been touched. For the adjacent posture, higher reaction times were found after stimulation of the interior as compared to the exterior fingers. This clearly indicates that, besides the effect of pure hand distance, reaction times were additionally affected by the spatial distance between tactile stimuli and conflictive response fields.

In experiment 2, the number and the size of response fields had no significant influence on reaction times. The possibility that the

absence of an effect was caused by the requirement of dividing attention between both hands was ruled out by experiment 3, in which the participants were instructed to attend only to one specific hand. Results in experiments 2 and 3 consist entirely in the absence of effects, raising doubts about their appropriate interpretation. However, since detection of the left hand was even faster during the right-enclosed as compared to the left-enclosed posture (which was contrary to our predictions) and also the interaction between postural conditions and attended hand in experiment 3 was directed contrary to our hypotheses, the results clearly show that the postural conditions did not affect reaction times in the expected way. This finding contradicts the previous conceptualization of response fields.

Taken together, the spatial distance between response fields and the spatial occurrence of tactile stimuli within these response fields had a significant impact on reaction times for tactile hand identification. Neither their number nor their size seems to have any effects on performance. The mental segmentation of peripersonal space into task-relevant subdivisions depends on the number of entities (here body parts), which have to be distinguished. A hand identification task implies two response alternatives, and therefore demands a spatial segmentation into at least two subdivisions. The number of response alternatives constitutes the minimum of required response fields. Assigning more than one spatial field to the same response alternative would naturally enhance the cognitive load, which should become manifest in increased reaction times. The results of experiment 2 and 3 therefore raise issues about the appropriateness of the first conceptualization of response fields described in study 1. In fact, experiments 2 and 3 of study 2 seem to indicate that the separation of two fingers of the same hand by fingers of the other hand does not result in a split-up of the associated response field.

Based on the results of study 2, we propose a modification of the previous conceptualization of response fields by withdrawing the assumption that one response field can be split into several smaller ones (see Discussion of study 1). The consequences of this modification with respect to the configuration of response fields representing the hands are illustrated in Figure 8. To identify a touched body part within an external frame of reference, each response alternative is represented by exactly one response field in peripersonal space. Depending on body posture and task

requirements, these response fields can overlap each other. According to this modified conceptualization, the right-enclosed and the left-enclosed posture both result in two overlapping response fields (Figure 8a). The overlap of response fields is absolutely equal for both postural conditions and for both hands. Assuming that the overlap of conflictive response fields constitutes a relevant factor modulating their discriminability, an assumption which is affirmed by experiment 1, it is coherent that the postural conditions had no effect on performance in experiment 2 and 3.

The results of experiments 2 and 3 suggest a modification, but do not call for a rejection of the concept of response fields, for its basic appropriateness is strongly supported by experiment 1, where reaction times were affected by the spatial distance between the stimulated fingers of different hands. Specifically the finding of

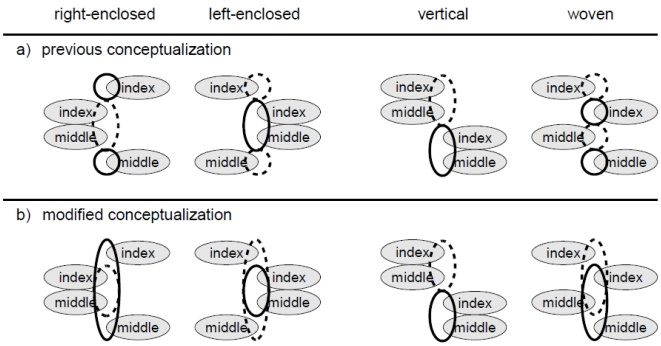

Figure 8 Comparison of **a)** the previous and **b)** the modified conceptualization of response fields on the basis of the postural conditions used in experiment 2 and 3 of study 2 (right-enclosed and left-enclosed) and the postural conditions used in study 1 and in Haggard et al. (2006) (vertical and woven). According to the previous version **(a)**, response fields for each hand differ in their number and size for the right-enclosed as compared to the left-enclosed and for the vertical as compared to the woven posture, predicting deviant performance for the first and the second pair of postures. According to the modified version **(b)**, the overlap between response fields is equal for the right-enclosed and the left-enclosed, but differs for the vertical and the woven posture, predicting equal performance for the first and deviant performance for the second pair of postures.

higher reaction times for the interior fingers (which were adjacent to a finger belonging to the other hand) than for the exterior fingers (which were more remote from the fingers of the other hand) in the adjacent posture demonstrates the existence of response fields. Tactile events are processed with respect to their external coordinates, and the reaction time needed to identify a stimulated body part depends on the spatial distance of the tactile stimulus from a non-stimulated body part (i.e., a spatial area representing a different response). The smaller the distance to a conflictive response field, the longer it takes to associate the stimulus with the correct response. It is of considerable importance here that the position of the hands itself does not change. The difference in reaction times cannot be accounted for by a variation of the distance between the hands themselves, but solely by the distance between the tactile stimulus and the untouched hand. This finding confirms the assumption of response fields and demonstrates the impact of the spatial distance between them.

In a recent study investigating the spatial representation of fingers, Overvliet et al. (2011) asked their participants to localize light tactile stimuli at the fingertips. Participants were instructed either to spread their fingers or to hold them close together, thereby varying the spatial distance between the stimulation sites. Interestingly, the spatial distance between fingers had no influence on the amount of localization errors towards neighboring fingers. The spatial proximity of untouched fingers to the tactile stimuli did not result in more mislocalizations towards those fingers, which seems contradictive to what was found in experiment 1 of the present study. However, in the study by Overvliet et al. (2011) participants had as much time as necessary to respond, whereas our participants were asked for speeded responses. As indicated by several studies, speeded response tasks are based on action-related spatial representations such as the body schema (Gallagher, 2005; Rossetti, 1998). Increased temporal delay between stimulus and response results in a cognitive evaluation of the response, and therefore reflects influences of the body image (Gallagher, 2005). Against this background, our results can be understood as reflecting the relevance of spatial distance for localization based on the body schema, while Overvliet et al. (2011) demonstrate that this relationship is diminished with respect to the body image. Differences between slow and speeded responses have been frequently reported in both

patient groups and healthy subjects (Goodale et al., 1994; Rossetti, Gaunet, & Thinus-Blanc, 1996; Rossetti, 1998).

Apart from the results of study 1 and 2, the modified version of the concept of response fields is capable to explain a variety of results reported in previous studies (Driver & Grossenbacher, 1996; Gallace & Spence, 2005; Haggard et al., 2006; Lloyd, 2007; Soto-Faraco et al., 2004). For example, it has been found in study 1 and in a study by Haggard et al. (2006) that performance in a tactile hand identification task decreases when the fingers of different hands are interleaved (woven posture) rather than grouped (vertical posture). Within the previous conceptualization of response fields this finding was explained by a split-up of response fields during the woven posture (Figure 8a). It is also compatible with the modified conceptualization, which states that the impairment during the woven posture is caused by an overlap of response fields for both hands (Figure 8b). A reversed effect of the vertical and the woven posture would be expected for the tactile identification of finger type, because regarding finger type it is the woven posture, in which the response fields are not overlapping. This dissociation between the postural conditions and task requirements could be confirmed in both experiments of study 1.

In spite of identical task demands, task complexity and participants between experiment 1 and 2 (differences consisted only in the postural conditions), overall reaction times were substantially shorter in experiment 1 (395ms) as compared to experiments 2 (441ms). This finding supports the assumption that the degree of overlap between response fields is the critical variable modulating their discriminability, because response fields were overlapping in experiment 2, but not in experiment 1 (Figure 8b).

The modified conceptualization of response fields states that the association between tactile stimuli and specific body parts is facilitated by a mental segmentation of peripersonal space into task-relevant subdivisions. These spatial areas constitute response fields, which are representing specific body parts and accordingly, in tactile identification tasks, specific response alternatives. Each response alternative is represented by exactly one response field, and the degree of overlap between them directly modulates the ability to associate a tactile stimulus with the touched body part.

4 Study 3: Ownership and Agency in the Rubber Hand Illusion

It has been investigated to which extent external objects like artificial hands can be incorporated into body representations. However, most studies dedicated to the effects of volitional motor control over external objects dealt with projected or mirrored images of own body parts.

Using the paradigm of the rubber hand illusion (RHI), we assessed the impact of passive tactile sensations and active volitional movements with respect to an artificial hand, which unambiguously was recognized as a body-extraneous object. In addition to phenomenal self-reports and motor responses, we introduced a new procedure for perceptual judgements enabling the assessment of proprioceptive drift and discrimination performance regarding perceived hand location.

RHI effects were comparable for passive touch and active movements, but characteristic discrepancies were found for motor responses. Motor responses were differently affected by the induction methods and performance was uncorrelated between both methods. These observations shed new light on inconsistent results concerning RHI effects on motor responses.

4.1 Introduction

The human body can be considered as the interface between the phenomenal self and the external world (Merleau-Ponty, 1945/1962). The sensation of tactile events at the body and motor control over body parts are the constituents for the development of a bodily self, i.e., the feeling of ‘being’ or ‘having’ a body (Tsakiris et al., 2006). The sensation of tactile events is a predominantly passive process and results in a feeling of ownership over the body, whereas motor

control implies an act of volition, involving a strong intentional component, and additionally causes a sense of agency (Gallagher, 2005; Haggard, 2008; Tsakiris et al., 2007b).

The aspect of tactile sensation has been thoroughly investigated using the rubber hand illusion (RHI). In the original version of this paradigm (Botvinick & Cohen, 1998), an artificial hand is placed visibly and in an anatomically plausible position in front of the participant, whose own hand is hidden from view. The experimenter then strokes both the artificial and the real hand in a synchronous manner with two identical paint brushes, which results in multisensory conflict between visual and proprioceptive information about hand posture. The touch is felt at a location different from where it is seen, and in order to solve this conflict, the perceived location of the own hand is shifted towards the location of the artificial hand. This phenomenon is generally referred to as proprioceptive drift and has often been used as a measure for the degree of incorporation of body-extraneous objects and the subjective feeling of ownership over an artificial limb (Kammers et al., 2009a; Tsakiris & Haggard, 2005).

The described procedure is based on passive tactile stimulation and refers to just one aspect of the bodily self, namely body ownership (Tsakiris et al., 2006; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007a). Only few studies implemented active motor control over finger movements of prosthetic hands to examine the sense of agency over body-extraneous objects (Azañón & Soto-Faraco, 2007; Dummer, Picot-Annand, Neal, & Moore, 2009; Kalckert & Ehrsson, 2012; Walsh, Moseley, Taylor, & Gandevia, 2011). Although several studies investigated the effect of displaced visual feedback regarding active finger movements, in nearly all of them visual feedback was presented either via video images of the real ipsilateral hand (Kammers et al., 2009b; Longo & Haggard, 2009; Newport et al., 2010; Tsakiris et al., 2006; Tsakiris et al., 2010) or via mirror reflections of the real contralateral hand (Holmes, Crozier, & Spence, 2004; Holmes & Spence, 2005; Holmes et al., 2006). These methods raise fundamental issues concerning the incorporation of body-extraneous objects into own body representations, because, strictly speaking, participants actually *are* looking at their real hand, even if the visual information is spatially displaced (Kalckert & Ehrsson, 2012). The critical question arises, whether the incorporation of a visually displaced own hand relies on the same

mechanisms as the incorporation of an unambiguously body-extraneous object (Bertamini, Berselli, Bode, Lawson, & Wong, 2011; Ijsselsteijn et al., 2006). The high familiarity regarding video displays and mirrors suggests the involvement of top-down processes, which have been shown to enhance the susceptibility to the RHI (Ehrsson et al., 2004; Holmes et al., 2006; Pavani et al., 2000; Tsakiris & Haggard, 2005).[10] The implementation of active motor control over prosthetic hands, which unambiguously will be considered as body-extraneous, is highly relevant to determine the relevance of a sense of agency for the incorporation of external objects and the development of a bodily self (Kalckert & Ehrsson, 2012).

Body representations depend on their functional relevance (Gallagher, 2005; Head & Holmes, 1911). The sensory information forming the basis for perceptual judgements (e.g., about body posture) is represented differently from the information being used for motor purposes (Dijkerman & de Haan, 2007; Kammers, van der Ham, & Dijkerman, 2006; Kammers et al., 2009a). Accordingly, the distinction between two types of body representations has been proposed, generally referred to as body schema and body image (Gallagher, 2005; Paillard, 1999). According to Gallagher's (2005) thorough description, which is based on the original conceptualization by Head & Holmes (1911), the body schema is defined as an implicit reference frame for the guidance of movements, whereas the body image consists in conscious perceptions and attitudes towards ones own body. The dissociation between body schema and body image is supported by clinical case studies (Buxbaum & Coslett, 2001; Head & Holmes, 1911; Paillard, 1999) as well as studies involving healthy participants (Cardinali et al., 2011; Kammers et al., 2006; Kammers et al., 2009a).

An approved and commonly used method to investigate the differential effects on body image and body schema consists in

[10] In another series of studies, movable artificial hands were presented within a virtual reality environment (Raz, Weiss, & Reiner, 2008; Sanchez-Vives, Spanlang, Frisoli, Bergamasco, & Slater, 2010; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2009). Although this method should diminish the influence of top-down effects, the familiarity regarding computer games still raises doubts about whether a virtual hand is perceived as an external object (in the same way as a material prosthetic hand). In spite of remarkable developments in virtual reality techniques, there are great differences between the neural processing of virtual as compared to material objects (Ijsselsteijn, de Kort, & Haans, 2006).

comparing the performance in perceptual and motor tasks (Cardinali et al., 2011; Kammers et al., 2006; Kammers et al., 2009a; Kammers et al., 2009b). This technique is derived from the assumption that perceptual judgements (e.g., verbal reports) rely on an intact body image, while motor responses (e.g., ballistic pointing movements) are based on body-schematic processes. With respect to the RHI, Kammers et al. (2009a; 2009b) found that perceptual judgements about hand posture were significantly biased towards the location of the artificial hand, while the accuracy of ballistic pointing movements towards the own hand was not impaired by the illusion. The authors concluded that the RHI involving passive tactile stimulation exclusively affects the body image (Kammers et al., 2009a).

However, the findings concerning the effects of the RHI on motor responses are inconsistent. Other studies did reveal significant effects on pointing and grasping movements, suggesting a distortion of the body schema (Botvinick & Cohen, 1998; Heed et al., 2011; Holmes et al., 2006; Kalckert & Ehrsson, 2012; Kammers, Kootker, Hogendoorn, & Dijkerman, 2010). These studies differ in many important aspects, which might explain the inconsistent results. First, in most studies the pointing targets were defined by visual rather than proprioceptive cues (e.g., Holmes et al., 2006; Kammers et al., 2009b), i.e., participants pointed with the stimulated hand towards a visually defined location in their environment rather than towards a proprioceptively defined location on their body (e.g., their non-stimulated hand, Kammers et al., 2009a). However, movements towards visual as compared to proprioceptively defined targets might be based on different mechanisms and different frames of reference. Second, some studies used passive tactile stimulation to induce the illusion (e.g., Botvinick & Cohen, 1998; Heed et al., 2011; Kammers et al., 2009a) and others implemented active voluntary finger movements of the artificial hand (e.g., Holmes et al., 2006.; Kalckert & Ehrsson, 2012). As pointed out by Kammers et al. (2009b), an induction method based on the sensory integration of motor commands, proprioception and visual feedback is more likely to interact with body-schematic representations (compared to an induction method based on the integration of tactile and visual information). Third and critically connected to the second point, the nature of the artificial hand varied across studies. As mentioned earlier, most studies implementing motor control over artificial

hands (and, with the exception of Kalckert & Ehrsson, 2012, all studies investigating its effect on motor responses) used video- or mirror-based versions of the RHI. To eliminate top-down processes caused by the high familiarity regarding video images and mirror reflections (Bertamini et al., 2011), the implementation of active motor control over prosthetic hands is of considerable importance.

In study 3 we therefore implemented a new technique to induce the RHI, involving voluntary motor control over the finger movements of an artificial hand, which unambiguously was recognized as body-extraneous (Kalckert & Ehrsson, 2012). Effects were quantified by altered performance in a perceptual and a motor task, as well as phenomenal self-reports, and were directly compared to those of the original induction method based on passive tactile stimulation of the own and the artificial hand.

4.2 Experiment

4.2.1 Methods

Participants 40 healthy participants (14 males; mean age was 24.5 years) were recruited from the University of Mannheim and the local community. They were either paid or received course credit. All were right-handed, as assessed by the revised Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave written informed consent to the experiment.

Experimental protocol The experimental set-up is depicted in Figure 9. The participants' hands were placed in a wooden framework (125cm*50cm*25cm). Vision of the right hand was prevented by an occluding screen. An artificial right hand made of wood and containing flexible joints at the digits was placed visibly in front of the participants, 15cm to the left of their right hand (measured from the index fingers). A skin-colored rubber glove was

slipped over the wooden hand. Participants were instructed to adjust their body midline halfway between the wooden hand and their own left hand, which was placed 31cm to the left of the artificial hand (Figure 9a). The index finger of the wooden hand could be lifted via a pneumatically driven plunger, which was controlled by a capacitive sensor placed beneath the participants' right index finger. The experimental set-up thus enabled the experience of agency over the index finger movements of the artificial hand.

The experiment was composed of four experimental conditions (synchronous and asynchronous touch, synchronous and asynchronous movements), each involving an induction phase (3min), a motor task (approx. 10sec), a perceptual task (approx. 2min) and an RHI questionnaire (approx. 1min). To exclude the possibility that perceptual responses were affected by the preceding motor responses, motor tasks were omitted for one third of all participants (N=13). No differences in the perceptual response were found depending on the presence or absence of a preceding motor response (see Results). The induction phases were specified by the method used to induce the RHI (passive vs. active) and the synchrony of associated stimuli (synchronous vs. asynchronous). The order of the experimental conditions was randomized across participants. Previous to the experimental conditions, a motor task (if included) and a perceptual task were performed as baseline measure.

Induction methods In the method of passive touch, the artificial index finger was stroked in synchrony with the unseen real index finger, using two identical paint brushes. This method is based on the integration of somatosensory and visual information and reflects the original procedure for the induction of the RHI (Botvinick & Cohen, 1998). In the active induction method, participants were instructed to voluntarily lift their right index finger every 3 to 5 seconds, approximately. These volitional movements were accompanied by corresponding synchronous movements of the artificial hand, which should result in a sense of agency for the latter (Kalckert & Ehrsson, 2012). This method is based on the integration of motor commands, proprioception and vision, and thus should be more likely to interact with the body representation that is related to action and movement, namely the body schema.

Both induction methods were performed in a synchronous and an asynchronous manner, in which a variable delay of 0.5 to 2 seconds was introduced between the respective events at the real and the artificial finger.

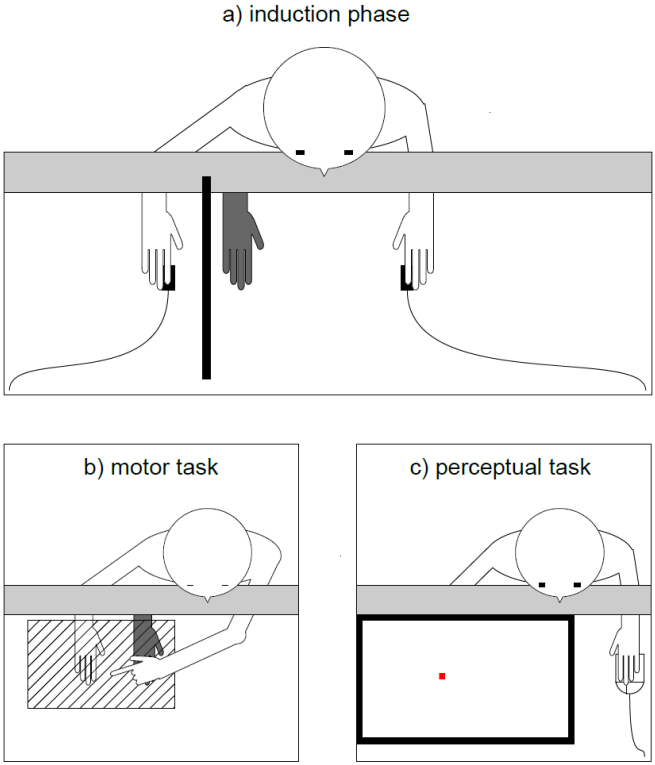

Figure 9 Experimental set-up. During the **a)** induction phase, vision of the own right hand was prevented by an occluding screen and participants were instructed to watch the artificial hand. In the **b)** motor task, participants pointed with eyes closed towards the location of their right index finger. In the **c)** perceptual task, participants indicated whether a series of dots on a horizontally placed computer monitor appeared to the right or to the left of their right index finger.

Motor task After the induction phase, participants were instructed to close their eyes. A wooden board containing a touch-sensitive area (26cm*17cm) was placed horizontally above their right hand (8cm above the table). When verbally prompted by the experimenter, participants moved their left (non-stimulated) index finger towards the position of their right index finger in a rapid, ballistic movement (Figure 9b). Once the board had been reached, no further corrections were allowed. Indicated locations were recorded by a camera (eSecure, USB 8MP 8 LED Webcam) fixed one meter above the participants' right hand. One pointing movement was performed in each of the four experimental conditions[11]. Individual accuracy of pointing was quantified by the variance of ten pointing movements, executed during the baseline. Pointing movements were always performed with eyes closed and practiced prior to the experiment.

Time points of movement initiations were recorded, enabling the calculation of movement times, which were used to control for the ballistic qualities of the pointing movements. Movement times deviating more than three standard deviations from the mean (i.e., higher than 609ms) were discarded.

Perceptual task After the motor task (participants kept their eyes close), the touch-sensitive board was removed and a computer monitor (52cm*29.5cm, LG Electronics Flatron W2443T) was placed horizontally above the artificial and the real right hand, completely occluding them from sight (Figure 9c). Participants then were asked to open their eyes and to judge the positions of a series of red dots appearing for 100ms on the screen (white background). Specifically, they had to indicate for each single dot, whether it was located to the left or to the right of their own right index finger. Each dot (2mm*2mm) was presented at one of ten possible positions, which were interspaced by 1cm and arranged along the horizontal plane in the middle of the monitor. To minimize ceiling and floor effects, the relative positions of the dots to the real right index finger were adjusted for each individual on the basis of the baseline data. Nevertheless, the data of two participants had to be excluded from analysis, because in at least one condition all dots were perceived at the same side relative to their own right index finger.

[11] For one participant, the recording in the synchronous condition of the active induction method failed.

Participants were asked to which side the dot would have to move to be exactly over their own right index finger. Responses were given via a computer mouse with the left hand. Participants were urged to respond as fast as possible. Responses later than 1s or earlier than 200ms after the dot's onset were discarded. The dots were presented ten times at each of the ten possible locations in randomized order, resulting in a total of 100 trials. The intertrial interval between the response and the appearance of the next dot was set to one second. Stimulus sequences were controlled using Presentation v14.2 (Neurobehavioral Systems, Inc., CA, USA).

Phenomenal self-reports After the perceptual task, the monitor was removed and participants completed an RHI questionnaire, consisting of nine statements about the subjective experience of the illusion. Agreement with these statements was indicated on a Likert scale involving seven steps (1 = strongly disagree, 7 = strongly agree). Due to the implementation of active finger movements, four items of the original questionnaire (Botvinick & Cohen, 1998) were pointless and were substituted by items taken from Longo et al. (2008) and Kammers et al. (2009a).

The questionnaire included four items which are related to the feeling of embodiment of the artificial hand (Longo et al., 2008) and five control items. Phenomenal embodiment was quantified by the mean response to the four embodiment-related items (items 1, 6, 7 and 8 in Table 6).

Statistical analysis According to the data of the perceptual responses, five logistic functions were fitted for each participant (baseline and four experimental conditions). These psychometric functions represent the probability of the response 'dot was left of index' depending on the dot's position. Statistical analysis was based on the 50% thresholds (estimate for the perceived location of the right index finger) and the slopes (estimate for discrimination performance) of the psychometric functions. For four participants the algorithm for logistic functions did not converge the data in one of the experimental conditions, resulting in extreme and implausible slopes (values exceeded five times the standard deviation of all slopes). These data were excluded from the analysis of the perceptual task.

Prior to analysis, individual baseline measures were subtracted from the data for the perceptual and the motor task. Due to the fact that the accuracy of pointing movements differs highly between individuals (Trojan et al., 2006), motor responses were weighted at the individual standard deviation of ten pointing movements during the baseline (ranging from 1.3cm to 3.1cm). All data were analyzed according to a linear mixed effects model (2*2 factorial design) including the factors induction method (passive touch vs. active movements) and synchrony (synchronous vs. asynchronous). Subjects were included as random factor.

Single items of the RHI questionnaire (Table 6) were analyzed with two-tailed t-tests for paired samples. Correlation analyses (one-tailed) were based on the differences between synchronous and asynchronous conditions.

Statistical analysis was conducted using R (version 2.13.1).

4.2.2 Results

Phenomenal self-reports Exclusively for the embodiment-related items (Longo et al., 2008), significant differences were found between the synchronous and the asynchronous conditions, independent of the induction method (items 1, 6, 7 and 8 in Table 6). Items 2 and 9 showed a difference for only one of the induction methods, and all other items did not reach a significant level for neither of the methods (Table 6).

A linear mixed effects model analysis of the mean responses to the four embodiment-related items revealed a significant main effect of synchrony ($F_{1/117}$=50.1, p<.001), but neither the main effect of induction method ($F_{1/117}$=2.3, p=.13) nor the interaction effect ($F_{1/117}$=.8, p=.37) was significant (Figure 10a).

The phenomenal self-reports were correlated between the induction methods (r=.30, t_{38}=1.9, p=.03), indicating that those participants, who reported a strong illusion after passive touch, were also more likely to report a strong illusion after active movements. Results are listed in Table 7.

Table 6 Mean responses (and standard deviation) to single items of the questionnaire. Items 1, 6, 7 and 8 are indicative for the embodiment of the artificial hand (Longo et al., 2008). Significant differences between synchronous and asynchronous conditions were calculated according to two-tailed t-tests for paired samples (*** p<.001, ** p<.01, * p<.05, n.s. p>.05).

	passive touch			active movements		
	sync.	async.	sign.	sync.	async.	sign.
1. It felt as if the artificial hand was my own hand.	4.7 (2)	2.7 (1.7)	***	4 (1.9)	2.6 (1.5)	***
2. It felt as if my real right hand was drifting toward the left (toward the artificial hand).	2.8 (1.9)	2.1 (1.3)	*	3.1 (1.7)	2.8 (1.8)	n.s.
3. It seemed as if I had two right hands.	2.3 (1.3)	2.6 (1.8)	n.s.	2.4 (1.6)	2.3 (1.5)	n.s.
4. My right hand felt numb.	3.5 (2.4)	3 (1.9)	n.s.	3.4 (2.2)	3 (2.1)	n.s.
5. It felt as if the artificial hand drifted slowly toward the right (toward my own right hand).	2 (1.3)	2.1 (1.3)	n.s.	2.3 (1.4)	1.9 (1.3)	n.s.
6. The artificial hand began to resemble my own right hand (in terms of shape, skin structure, etc.)	3.5 (2.1)	2.8 (1.7)	*	3.2 (2)	2.4 (1.8)	*
7. It seemed as if the artificial hand was part of my body.	4.6 (2)	2.7 (1.8)	***	3.8 (2.1)	2.7 (1.7)	***
8. It seemed as if I looked directly at my own hand, and not at an artificial one.	3.9 (2)	2.4 (1.7)	***	3.6 (1.9)	2.4 (1.5)	***
9. It felt as if the artificial hand and my own right hand lay closer to each other (compared to the beginning of the trial).	3.6 (1.9)	3.4 (1.9)	n.s.	3.6 (2)	3.1 (1.8)	*

Perceptual task To assure that perceptual responses were not influenced by the preceding motor responses, we compared the data of participants who performed a motor task previous to the perceptual task (N=22) with the data of participants for which the motor tasks were omitted (N=12). Two-tailed t-tests revealed no significant differences in the perceptual task between these groups,

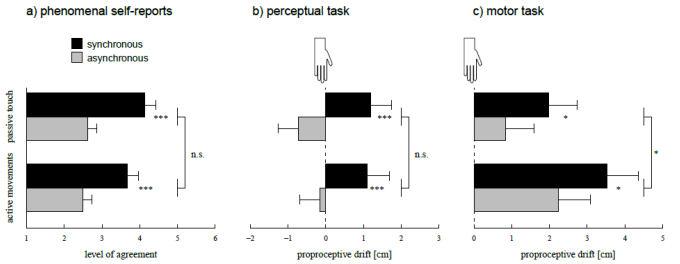

Figure 10 Empirical data according to **a)** the phenomenal self-reports, **b)** the perceptual task and **c)** the motor task for the passive (top) and the active induction method (bottom). Dashed lines in the perceptual and the motor task (value of zero) indicate the perceived location of the right index finger during the baseline. Error bars show standard errors across subjects.

neither for the baseline nor for any of the four experimental conditions (all p>.1). Furthermore, separate analyses for both groups showed equivalent results for the perceptual task. The motor task did not affect subsequent perceptual responses.

Table 7 Results according to linear mixed effects models for phenomenal self-reports, perceptual judgements and motor responses. (*** p<.001, ** p<.01, * p<.05, n.s. p>.10).

	phenomenal self-reports	perceptual task		motor task
linear mixed effects model		perceived location (thresholds)	discrimination performance (slopes)	
synchrony	$F_{1/117}$=50.1, ***	$F_{1/99}$=27.1, ***	$F_{1/99}$=5.0, *	$F_{1/76}$=4.9, *
induction	$F_{1/117}$=2.3, n.s.	$F_{1/99}$=0.6, n.s.	$F_{1/99}$=0.6, n.s.	$F_{1/76}$=6.8, *
synchrony*induction	$F_{1/117}$=0.8, n.s.	$F_{1/99}$=1.3, n.s.	$F_{1/99}$=1.4, n.s.	$F_{1/76}$<0.1, n.s.
correlation (between passive and active induction)	r=.30, t_{38}=1.9, *	r=.43, t_{32}=2.7, **		r=.01,t_{23}<0.1,n.s

Synchrony had a significant effect on the proprioceptive drift towards the artificial hand ($F_{1/99}$=27.1, p<.001), which was higher for the synchronous as compared to the asynchronous conditions (Figure 10b). The induction method itself had no influence on the magnitude of the proprioceptive drift ($F_{1/99}$=0.6, p=.44). The interaction between induction method and synchrony was not significant ($F_{1/99}$=1.3, p=.27), showing that both induction methods were equally qualified to elicit a proprioceptive drift in the perceptual task. The results are listed in Table 7, and averaged psychometric functions for the perceptual judgements are depicted in Figure 11.

Again, there was a significant correlation between the RHI effects after passive touch and those after active movements, i.e., the same participants demonstrated either a small or a large proprioceptive drift for the passive and the active induction method (r=.43, t_{32}=2.7, p<.01).

One advantage of the perceptual task implemented here is that it enables the assessment of discrimination performance, quantified by the slopes of the psychometric functions (Figure 11). The data for discrimination performance reflect the results for perceived location: a significant main effect was found for synchrony ($F_{1/99}$=5.0, p=.03), while neither the induction method ($F_{1/99}$=0.5, p=.46) nor its interaction with synchrony ($F_{1/99}$=1.4, p=.24) had a significant effect on the discrimination performance (Table 7). The mean of slopes for synchronous conditions was 0.35 and for the asynchronous conditions 0.30, indicating that discrimination performance was better after synchronous as compared to asynchronous stimulation.

Motor task The ballistic qualities of the pointing movements were confirmed by a mean movement time of 361ms (ranging from 189ms to 536ms).

Again, synchrony had a significant effect on task performance ($F_{1/76}$=4.9, p=.02). The proprioceptive drift towards the artificial hand was higher for the synchronous than for the asynchronous conditions (Figure 10c). In contrast to the phenomenal self-reports and the perceptual task (Table 7), motor responses were significantly affected by the induction method ($F_{1/76}$=6.8, p=.01), indicating that pointing movements were biased towards the artificial hand after active as compared to passive induction. No interaction between synchrony and induction method was found ($F_{1/76}$<.1, p>.5).

Furthermore, performance in the motor task was not correlated between the induction methods, as it was the case for phenomenal self-reports and perceptual judgements (Table 7). Participants showing a relatively large pointing bias towards the artificial hand after passive touch were not necessarily those who showed a comparable pointing bias after active movements (r=.006, t_{23}=.03, p=.49).

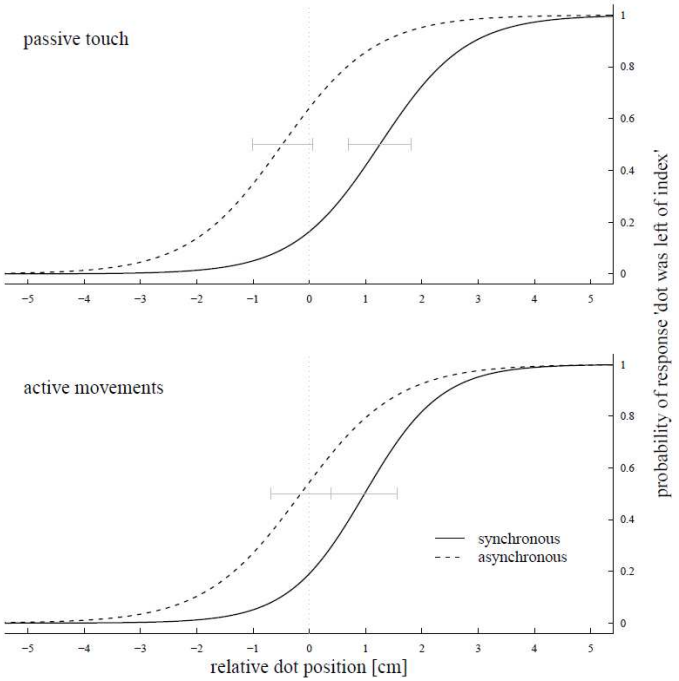

Figure 11 Psychometric (logistic) functions for the perceptual task after passive (top) and active induction (bottom), based on averaged individual parameters. The abscissa indicates the dot's position relative to the perceived location of the right index finger during the baseline (dashed vertical line). Error bars show standard errors across subjects.

4.3 Discussion

In study 3 we implemented a version of the RHI paradigm based on active voluntary movements of body-extraneous objects. This was achieved by imposing voluntary control over finger movements of an artificial hand, which was unambiguously recognized as body-extraneous. Alterations of body representations were quantified by means of phenomenal self-reports, perceptual judgements and motor responses, and directly compared to corresponding effects elicited by a mere perceptual version of the RHI (Botvinick & Cohen, 1998).

For both the passive and the active induction method, we found substantial differences between the synchronous and the asynchronous condition in all three measures (Figure 10). The type of induction exclusively affected motor responses, resulting in a larger proprioceptive drift after active as compared to passive induction. Phenomenal self-reports and perceptual judgements were not influenced by the induction method. Furthermore, differences between the synchronous and the asynchronous conditions in the motor task were not correlated between passive and active induction, as it was the case for phenomenal self-reports and perceptual judgements.

Since active control over (unambiguously) body-extraneous objects has rarely been implemented in experimental settings (see Introduction and Kalckert & Ehrsson, 2012), the comparable effects on phenomenal self-reports and perceptual responses are particularly important to validate the experimental set-up used in study 3. For both the phenomenal self-reports and the perceptual task, neither the main effect of induction method nor its interaction with synchrony was significant, indicating that both methods were equally qualified to induce the illusion (Figure 10 and Table 7). The RHI effect of passive touch on the motor task (i.e., pointing movements) contrasts with the results of Kammers et al. (2009a; 2009b), who found motor responses to be unaffected by the passive induction method. These authors concluded that the passive induction method exclusively affects the body image, while body-schematic representations are resistant against this kind of manipulation (Kammers et al., 2009a)

The inconsistencies between the results from Kammers et al. (2009a; 2009b) and study 3 reflect the diverse findings in the scientific literature on this issue. While the effects on phenomenal

self-reports and perceptual responses are relatively consistent across several investigations (Botvinick & Cohen, 1998; Dummer et al., 2009; Kammers et al., 2009a), many studies did reveal inconsistent evidence as to whether motor responses are affected by the RHI (Heed et al., 2011; Holmes et al., 2006; Kalckert & Ehrsson, 2012; Kammers et al., 2009a; Kammers et al., 2009b; Kammers et al., 2010). In study 3, two differences between the passive and the active induction method were found, which were specific for the motor task, and therefore should be considered for their explanatory value with regard to the inconsistencies on that issue.

First, the performance in the motor task was not correlated between both induction methods, as it was the case with respect to the phenomenal self-reports and the perceptual task. The absence of this correlation indicates that individuals who are more susceptible to the passive induction method (quantified by pointing errors) are not necessarily more susceptible to the active induction method.

Second, there was a significant main effect of the induction method on the performance in the motor task. In both the synchronous and the asynchronous condition, pointing movements were more biased towards the artificial hand when the illusion was induced by active movements as compared to passive touch (Figure 10c). A similar finding was reported by Kammers et al. (2009b), who found a significant interaction between induction method and response type, indicating that perceptual responses were more affected by the passive induction method, while the active induction method had a pronounced influence on motor responses. A possible explanation for this specific result lies in the existence of shared representations for executed and observed movements (Decety & Sommerville, 2003; Georgieff & Jeannerod, 1998; Grèzes & Decety, 2001). A partial overlap between cortical networks, which are activated both by the self-execution of specific actions and by the mere observation of these actions executed by another agent, show that to a certain degree observed movements are processed in the same way as self-executed movements (Georgieff & Jeannerod, 1998). According to these considerations, it is well comprehensible that the motor representations underlying pointing movements are influenced even by asynchronous movements of an artificial limb, which nevertheless might be regarded as body-extraneous.

The overall pointing bias towards the artificial hand after active as compared to passive induction might as well reflect a tendency to

execute shorter pointing movements after pre-activation of the motor system. This possibility cannot be refuted on the basis of the present data, however, it seems implausible, because an influence of motor pre-activation was not reported in similar studies (Kalckert & Ehrsson, 2012; Kammers et al., 2009b).

The absence of correlation between the passive and the active induction method suggests that body-schematic alterations are less stable than alterations of the body image. Although an effect of synchrony on pointing movements was found for both induction methods, these effects are based on varying subsets of participants. Unlike the effects on the perceptual task, to which individuals seem to be susceptible in a reliable manner, effects on the motor task are relatively short-lived (Rossetti, 1998). These considerations are relevant to explain inconsistent findings with respect to motor tasks. For example, Kammers et al. (2009b) previously compared the effects of passive and active induction of the RHI on perceptual and motor responses, and did not find a difference between synchronous and asynchronous conditions on motor responses, neither for the passive nor the active induction method. Two differences in the experimental design between study 3 and Kammers et al. (2009b) seem particularly relevant to explain this deviant result. First, our participants pointed with their non-stimulated towards the stimulated hand, directly indicating its perceived position, while in Kammers et al. (2009b), pointing movements were executed with the stimulated hand towards a visually defined external target, and the proprioceptive drift was assessed indirectly by inferring the perceived hand position from endpoint errors. Second, Kammers et al. (2009b) used a video-based version of the RHI. As discussed initially, participants are well aware of the non-materiality of 2D video-displayed images (Ijsselsteijn et al., 2006), which raises issues concerning the incorporation of external objects into body representations. Furthermore, top-down processes might interfere with the bottom-up effects of synchronous stimulation (or movements), because participants know that they are indeed looking at (an image of) their own hand (Kalckert & Ehrsson, 2012).

To our knowledge, this is the first study applying the technique of fitting psychometric functions to judgements about hand location within the RHI. A valuable advantage of this technique consists in the assessment of discrimination performance, which can be

quantified by the slopes of psychometric functions. This is an important aspect, because decreased discrimination performance would affect the reliability of judgements on perceived hand location, and it seems plausible to assume decreased discrimination performance during the RHI. Our results demonstrate that discrimination performance is slightly increased after synchronous as compared to asynchronous conditions (Figure 11). Furthermore, it is shown that both the passive and the active induction method are equally qualified to induce this gain in discrimination performance (Table 7).

Taken together, two characteristic differences were found between the induction via passive tactile sensations and active volitional movements, exclusively relating to the performance in the motor task. RHI specific effects were not correlated between the passive and the active induction method, and an overall pointing bias towards the artificial hand (i.e., independent of synchrony) was found for the active as compared to the passive induction method.

The results of study 3 demonstrate that both perceptual judgements (presumably relying on an intact body image) and motor responses (presumably based on body-schematic processes) about body posture are affected by the passive and the active induction method for the RHI. Both passive tactile sensations and active volitional movements result in a phenomenal incorporation of an artificial hand and in a proprioceptive drift of the own towards the artificial hand. Nevertheless, characteristic differences concerning the motor task were revealed, causing doubts on the reliability of motor responses and thereby providing an explanation for the inconsistent findings in the scientific literature on this issue.

5 Study 4: Anatomical Constraints for Body Representations

The notion of a congenital body-model has been supported by clinical observations of aplasic phantoms and experimental studies revealing anatomical constraints for changes in body representations, while other studies suggest a remarkable flexibility of body representations even exceeding *a priori* assumptions regarding body appearance and anatomy (e.g., the subjective embodiment of a third arm).

Using the rubber hand illusion (RHI), in which a visible artificial hand is touched synchronously with the participant's unseen own hand, we examined the role of anatomical congruence between stimuli at the artificial and the own hand. Based on considerations according to which the influence of anatomical congruence might differ for the sense of ownership and the sense of agency, two versions of the RHI paradigm were implemented, involving either passive tactile stimulation or active voluntary movements.

5.1 Introduction

The development of a bodily self (i.e., the conscious perception of 'being' or 'having' a body) is derived from two different aspects concerning the relation between the body and the external world, commonly referred to as body ownership and agency (Gallagher, 2000; Gallese & Sinigaglia, 2010; Tsakiris et al., 2006; Tsakiris et al., 2007b). Body ownership denotes the sense that one's own body is the source of sensations (Tsakiris et al., 2006). External events at the bodily borders are directly perceived as somatic sensations, which can be described by the notion 'What happens to this body, happens to *me*'.

Agency reflects the fact that phenomenal intentions to modify the external world can only be realized by controlling one's own body movements (Gallese & Sinigaglia, 2010; Tsakiris et al., 2006). Intentional changes within the environment (e.g., lifting a cup) can only be caused indirectly, i.e., mediated by motor control over body parts (moving the hand towards the cup, grabbing it, etc.). This can be illustrated by the phrase '*I* can affect the world only by means of this body'. These two aspects (direct sensation and direct motor control) contribute to the perception of a strong connection between the own body and the phenomenal self, and ultimately to the development of a bodily self.

Both the sense of ownership and the sense of agency can be manipulated within the paradigm of the rubber hand illusion (RHI), which is based on the multisensory integration of conflicting information about body posture (Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2012; Kammers et al., 2009b; Tsakiris et al., 2006; Tsakiris et al., 2010). In the RHI, an artificial hand is placed visibly in front of the participant, whose own hand is hidden from view. By synchronously touching the artificial and the real hand, or by synchronizing the movements of both hands, a multisensory conflict between visual and proprioceptive information about hand posture can be induced, resulting in the illusory feeling of ownership and/or agency over the artificial hand. The subjective feeling of embodiment is accompanied by a shift of the perceived location of the own hand towards the artificial hand, a phenomenon which generally is referred to as proprioceptive drift (Kammers et al., 2009a; Tsakiris et al., 2006).

Many studies indicated that the embodiment of the artificial hand depends on an anatomically correct appearance (Holmes et al., 2006) and the physical connectedness to the body (Ehrsson et al., 2004; Pavani et al., 2000), supporting the assumption of a congenital body-model (Costantini & Haggard, 2007; De Preester & Tsakiris, 2009; Tsakiris & Haggard, 2005). On the other hand, remarkable changes in body representations have been reported after visual exposure to anatomically implausible (e.g., a lengthened arm, Schaefer et al., 2007) and even after anatomically impossible body configurations (e.g., a third arm, Guterstam et al., 2011; Schaefer et al., 2009).

In a study by Schaefer et al. (2006), participants received tactile stimuli at the little finger of their left hand while watching synchronous stimulations on the thumb of a virtual hand. Due to the

anatomical incongruence, participants reported a referred sensation (i.e., they felt the touches on their thumb instead of their little finger), the degree of which was significantly correlated with short-term alterations in the topography of the primary somatosensory cortex. This raises the question whether alterations of body representations depend more on the consistency of visual feedback rather than on its anatomical congruence, because in the study by Schaefer et al. (2006) the somatosensory effects of the visible stimuli were absolutely reliable and predictable. In other words, the visual feedback was anatomically incongruent in a very consistent manner.

The predictability of bodily effects is an important factor for the emergence of a sense of agency, even if those effects are discordant with efferent motor commands (Sato, 2009; Wegner & Wheatley, 1999; Wegner, Sparrow, & Winerman, 2004). Therefore, it seems plausible that a consistent coupling between motor commands and bodily effects can compensate for their anatomical incongruence. Several studies suggested a specific role of motor activity for modulations of body representations (Braun et al., 2001; Moseley & Brugger, 2009; Schaefer et al., 2005), but studies on the processing of anatomically incongruent movements are rare (Fink et al., 1999). Nevertheless, there is evidence that humans are extremely sensitive to incongruent visual feedback about their own movements at a very early developmental stage (Morgan & Rochat, 1997).

The influence of predictability on the sense of agency has been investigated mainly in terms of perceived causation of external effects (e.g., sounds or visual stimuli), adopting a body-independent definition of agency (Aarts, Custers, & Wegner, 2005; Linser & Goschke, 2007; Moore & Haggard, 2008; Sato & Yasuda, 2005; Wenke, Fleming, & Haggard, 2010). However, perceived control over own body movements and perceived control over body-external events are very different aspects of agency (Sartre, 1943/1958; Wegner et al., 2004). This important distinction was referred to by Sartre, when he recognized that ‘I use my pen in order to form letters but not *my* hand in order to hold the pen. I am not in relation to my hand in the same utilizing attitude as I am in relation to the pen; I *am* my hand.’ (Sartre, 1943/1958, p.323). On the same account, Wegner et al. (2004) suggested the distinction of authorship processing (agency for body movements) and causal attribution (agency for environmental effects). This distinction is especially relevant for the investigation of the dynamic qualities of body representations. In

study 4 we focus on perceived agency for body movements, without accounting for the indirect external effects of those movements.

Study 4 was conducted to investigate the impact of anatomical congruence and coupling consistency on changes in body representations. We implemented a passive and an active version of the RHI paradigm, based on passive tactile stimulation or active voluntary movements of the artificial and the real hand, respectively. Anatomical incongruence was realized by a reversed coupling of index and middle fingers of the artificial and the real hand, and coupling inconsistency by a random variation of congruent and incongruent coupling.

According to the assumption of a congenital body-model, the embodiment of the artificial hand should depend on the anatomical congruence, but not on coupling consistency. Embodiment of the artificial hand was quantified by phenomenal self-reports and a perceptual measure of proprioceptive drift.

5.2 Experiment

5.2.1 Methods

Participants 28 right-handed participants (7 males, mean age was 27.8 years) were recruited from the University of Mannheim and the local community. Participation was compensated either monetarily or with course credits (for psychology students). All participants gave written informed consent to the experiment.

Experimental set-up Participants sat at a desk and placed their hands in a wooden framework (125cm*50cm*25cm). Vision of their right hand was prevented by an occluding screen. An artificial right hand made of wood and containing flexible joints at the sockets of the digits was placed visibly in front of the participants, 15cm to the left of their own right hand (measured from the index fingers). A

skin-colored rubber glove was slipped over the artificial hand. Participants were instructed to adjust their body midline halfway between the artificial right hand and their own left hand, which was placed 31cm to the left of the artificial hand. Body posture and arrangement of real and artificial hands were identical to study 3, so a graphical depiction of the experimental set-up is provided by Figure 9a and 9c. Index and middle fingers of the artificial hand could be lifted and lowered via pneumatically driven plungers, which were embedded in the framework. Invisible to the participants, the plungers were controlled by capacitive sensors placed beneath the participants' right index and middle fingers. In this vein, the experimental set-up enabled the experience of direct control over the finger movements of the artificial hand.

Experimental conditions For both the passive and the active induction method, four experimental conditions were implemented (Table 8).

In the congruent condition, the participants' right hand and the artificial hand were stroked synchronously with two paint brushes in an anatomically congruent manner (i.e., either both index fingers or both middle fingers). The incongruent condition consisted in synchronous stroking of anatomically unrelated fingers (i.e., the real index and the artificial middle finger or the real middle and the artificial index finger). Importantly, in both the congruent and the incongruent condition the combination of real and artificial fingers, whether anatomically congruent or not, was invariable, and therefore predictable, throughout the particular induction phases.

In the inconsistent condition, the consistency of coupling between real and artificial fingers was eliminated by unsystematically alternating the combination of real and artificial fingers. Tactile stimuli were applied synchronously to the real and the artificial hand in an anatomically correct or incorrect manner. A control condition including asynchronous stimulation served as a reference for the congruent condition to quantify basic RHI effects. Apart from a temporal delay (distributed between 0.5 and 2 seconds) between corresponding stimuli at the real and the artificial hand, the control condition was identical to the congruent condition. In all conditions involving passive touch, stimulus combinations were applied every 5 to 10 seconds.

Table 8 Experimental conditions adapted to the passive and the active induction method in study 4. Associated pairs of conditions for testing the impact of temporal synchrony, anatomical congruence and coupling consistency are shaded accordingly.

experimental condition	temporal synchrony	anatomical congruence	coupling consistency
control	asynchronous		
congruent	synchronous	congruent	consistent
incongruent	synchronous	incongruent	consistent
inconsistent	synchronous	incongruent	inconsistent

To compare the RHI effects after passive touch with those after active movements, four analogous conditions were implemented for the induction by active movements. Finger movements of the participants' right hand were accompanied by synchronous finger movements of the artificial hand. The coupling between real and artificial fingers was either anatomically congruent, incongruent or unsystematically varying (inconsistent). In the control condition, congruent finger movements of the artificial hand were delayed by 0.5 to 2 seconds. In all movement conditions, participants were instructed to shortly lift either their index or their middle finger (but not both at the same time), approximately every 3 to 5 seconds. Furthermore, they were asked to maintain an approximately equal ratio between movements of the index and the middle finger.

Each of the resulting eight experimental conditions involved an induction phase (1.5min), the assessment of proprioceptive drift (2min) and the completion of a questionnaire (approx. 1min). All conditions of the same induction method were performed successively. The order of induction method as well as the order of conditions (within each method) was randomized across subjects, but kept constant for both methods (within subjects).

Proprioceptive drift The procedure for the assessment of proprioceptive drift was executed previous to the experiment

(baseline) and after each of the eight experimental conditions. After the induction phase, participants were instructed to close their eyes. The experimenter removed the occluding screen and placed a computer monitor (52cm*29.5cm, LG Electronics Flatron W2443T) horizontally above the artificial and the real right hand, completely occluding them from sight (Figure 9c). Participants then were asked to open their eyes and to judge the positions of a series of red dots appearing for 100ms on the screen (white background). Specifically, they had to indicate for each single dot, whether it was located to the left or to the right of their own right index finger. Each dot (2mm*2mm) was presented at one of fourteen possible positions, which were interspaced by 1cm and arranged along the horizontal plane in the middle of the monitor. To minimize ceiling and floor effects, the relative positions of the dots to the real right index finger were adjusted for each individual on the basis of the baseline data.

Participants were asked to which side the dot would have to move to be exactly over their right index finger. Responses were given via a computer mouse with the left hand. The left button indicated that the participants' index finger was perceived at the left side of the dot, and the right button indicated that it was perceived to the right of the dot. Participants were urged to respond as fast as possible. Responses later than 1s or earlier than 200ms from the dot's onset were discarded.

The dots were presented seven times at each of the 14 possible locations in randomized order, resulting in a total of 98 trials. The intertrial interval between the response and the appearance of the next dot was set to 1s. This procedure enables the assessment of discrimination performance and has been approved in study 3. Stimulus sequences were controlled using Presentation v14.2 (Neurobehavioral Systems, Inc., CA, USA).

Phenomenal self-reports After the assessment of proprioceptive drift, participants completed an RHI questionnaire, consisting of nine statements regarding the subjective experience of the illusion during the induction phase. Agreement with these statements was indicated on a Likert scale involving seven steps (-3 = strongly disagree, 3 = strongly agree). Questionnaire items were selected from an extensive psychometric study (Longo et al., 2008) and are listed in Table 9. According to Longo et al. (2008), four items referred to the embodiment of the artificial hand (items 1 and 6 in Table 9

representing body ownership and items 2 and 7 representing body agency[12]), two items targeted the affective valence of the experience (items 3 and 8) and three items served as control questions (items 4, 5 and 9).

Table 9 Item labels used in study 4 and their categories according to Longo et al. (2008).

item label	item category
1. It felt as if the artificial hand was my own hand.	embodiment (ownership)
2. It seemed like I could grab something with the artificial hand.	embodiment (agency)
3. I found that experience enjoyable.	affect
4. It seemed like I had three hands.	control question
5. I had the sensation that my hand was numb.	control question
6. It seemed like the artificial hand was part of my body.	embodiment (ownership)
7. It seemed like I could make a fist with the artificial hand.	embodiment (agency)
8. I found that experience interesting.	affect
9. It seemed like my hand had disappeared.	control question

Statistical analysis Proprioceptive drift was quantified by means of psychometric functions, calculated on the basis of the data from the perceptual task. Logistic functions were fitted for each of the experimental conditions and the baseline, representing the probability of the response 'dot was left of index' depending on the dot's position. The 50% thresholds of these psychometric functions were used as an estimate for the perceived location of the right index finger, and the slopes of the same functions served as a measure for discrimination performance. Regarding the 50% thresholds, individual baseline values were subtracted from the values for the experimental conditions.

[12] Due to the implementation of controlled finger movements of the artificial hand, the agency items tested in Longo et al. (2008) were not appropriate and were modified for study 4 (see Table 9).

The questionnaire data were averaged according to the subscales ‘ownership’, ‘agency’, ‘affect’ and ‘control’ (Table 9) for each participant (Longo et al., 2008).

Statistical analysis was based on linear mixed effects models as implemented in package ‘nlme’ for R software (version 2.13.1). Subjects were specified as random factor.

5.2.2 Results

Temporal synchrony According to conventions within RHI studies, the general efficiency of the experimental set-up was verified by comparing the effects of synchronous and asynchronous touch/movements (Figure 12). Linear mixed effects models including the factors ‘synchrony’ (congruent condition vs. control condition) and ‘induction method’ (passive touch vs. active movements) revealed a significant main effect of synchrony on the perceptual task ($F_{1/81}$=10.6, p=.002), the embodiment-related questionnaire items (ownership: $F_{1/81}$=55.9, p<.001; agency:

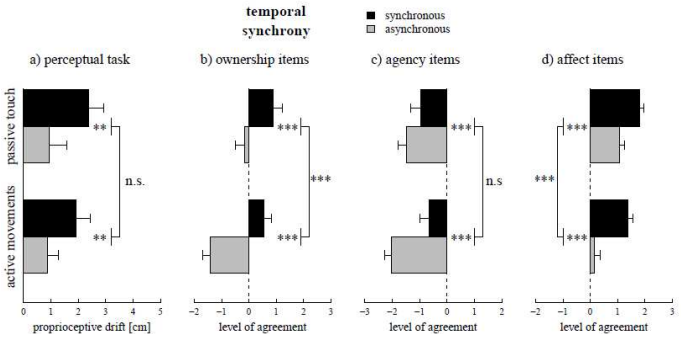

Figure 12 Comparison between the congruent condition (black bars) and the control condition (grey bars), which differed exclusively in the temporal synchrony between touches at (or movements of) the real and the artificial hand.

$F_{1/81}$=30.0, p<.001) and the affect-related questionnaire items ($F_{1/81}$=53.7, p<.001). Importantly, synchrony did not affect the responses to control items ($F_{1/81}$=1.2, p=.28).

The main effect of induction method was significant only for the ownership and the affect items of the questionnaire (ownership: $F_{1/81}$=16.2, p<.001; affect: $F_{1/81}$=24.3, p<.001), but not for the agency items ($F_{1/81}$=0.5, p=.49) and the perceptual task ($F_{1/81}$=0.5, p=.49). Perceived ownership of the artificial hand and affective valence were higher after passive touch than after active movements, independent of synchrony (Figure 12).

Significant interactions between synchrony and induction method regarding embodiment-related items (ownership: $F_{1/81}$=5.1, p=.03; agency: $F_{1/81}$=5.7, p=.02) indicate that the effect of synchrony was more pronounced after active movements than after passive touch (Figure 12). This advantage of the active induction method was restricted to phenomenal self-reports and could not be verified regarding the perceptual task ($F_{1/81}$=0.3, p>=.5). Also no interaction was found for affective valence ($F_{1/81}$=3.0, p=.09).

Anatomical congruence To examine the importance of an anatomically congruent mapping between the own and the artificial fingers, we compared the effects of the congruent condition with those of the incongruent condition (Figure 13). A significant main

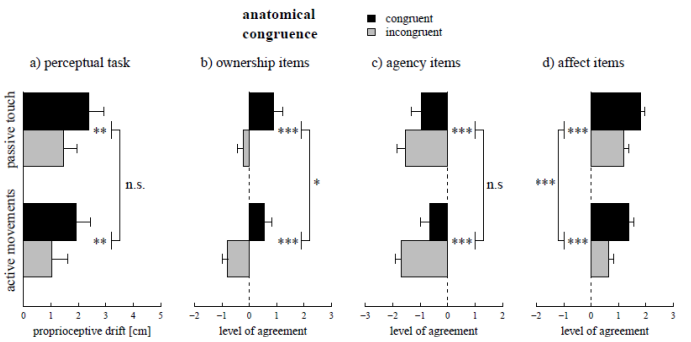

Figure 13 Comparison between the congruent condition (black bars) and the incongruent condition (grey bars), which differed exclusively in the anatomical congruence of coupling between fingers of the real and the artificial hand.

effect of anatomical congruence was found for the perceptual task ($F_{1/81}$=6.7, p=.01) and the embodiment-related and affect-related questionnaire items (ownership: $F_{1/81}$=29.5, p<.001; agency: $F_{1/81}$=15.4, p<.001; affect: $F_{1/81}$=30.9, p<.001). Proprioceptive drift, perceived embodiment and affective valence were higher after congruent conditions.

Again, only the ownership and affect items were affected by the induction method (perceptual task: $F_{1/81}$=1.5, p=.22; ownership: $F_{1/81}$=4.3, p=.04; agency: $F_{1/81}$=0.2, p>.5; affect: $F_{1/81}$=15.6, p<.001), showing a higher degree of perceived ownership and affective valence after the passive as compared to the active induction method (Figure 13). Contrary to the considerations regarding a differential impact of anatomical congruence for passive touch and active movements, no interactions between anatomical congruence and the induction methods were found (perceptual task: $F_{1/81}$<0.1, p>.5; ownership: $F_{1/81}$=0.2, p>.5; agency: $F_{1/81}$=1.2, p=.28; affect: $F_{1/81}$=0.2, p>.5).

Coupling consistency The impact of consistency with respect to the coupling between own and artificial fingers was assessed by a comparison between the incongruent and the inconsistent conditions (Figure 14). Both of these experimental conditions involved anatomically incongruent feedback, but in the incongruent

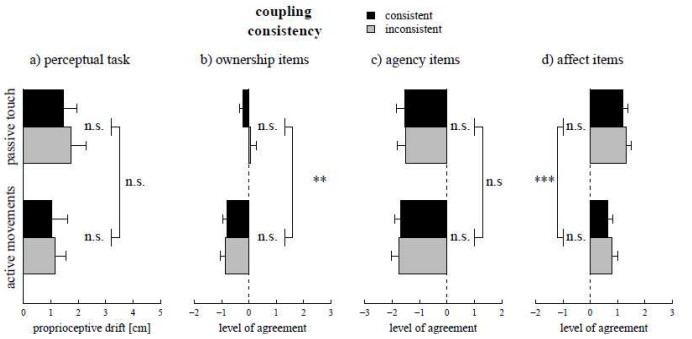

Figure 14 Comparison between the incongruent condition (black bars) and the inconsistent condition (grey bars), which differed exclusively in the consistency of coupling between fingers of the real and the artificial hand.

conditions, the coupling of artificial and real fingers was invariable and absolutely reliable, while in the inconsistent condition, the coupling between own and artificial fingers changed at random. Neither for the perceptual task ($F_{1/81}$=0.3, p>.5) nor for the embodiment-related and affect-related questionnaire items (ownership: $F_{1/81}$=0.2, p>.5; agency: $F_{1/81}$<0.1, p>.5; affect: $F_{1/81}$=1.3, p=.25) a main effect of coupling consistency could be confirmed.

Again, the method of induction had a selective effect on ownership and affect items (ownership: $F_{1/81}$=11.4, p=.001; affect: $F_{1/81}$=16.0, p<.001), while neither the perceptual task ($F_{1/81}$=1.5, p=.22) nor the agency items ($F_{1/81}$=1.0, p=.32) were influenced by this factor (Figure 14). No interactions between coupling consistency and induction method were found (perceptual task: $F_{1/81}$<0.1, p>.5; ownership: $F_{1/81}$=0.6, p=.42; agency: $F_{1/81}$<0.1, p>.5; affect: $F_{1/81}$<0.1, p>.5).

Discrimination performance Regarding discrimination performance, quantified by the slopes of the psychometric functions, which were calculated according to the data from the perceptual task, no significant differences were found throughout study 4 (all p>.05). Mean slope for all experimental conditions was .22, ranging between .20 and .25. Thus, the proprioceptive drifts reported above were not accompanied by a higher or lower certainty regarding the perceived location of the own right index finger.

5.3 Discussion

Study 4 aimed at investigating the importance of anatomical congruence and coupling consistency for alterations of body representations during the RHI (Botvinick & Cohen, 1998). The concept of a congenital body-model (De Preester & Tsakiris, 2009; Tsakiris & Haggard, 2005) predicts a high impact of anatomical congruence between visual and sensorimotor information about the own body, but several experimental findings challenge this view by claiming that constraints regarding body appearance and anatomy can be overcome (Guterstam et al., 2011; Schaefer et al., 2007;

Schaefer et al., 2009). The constitutive factor might rather consist in the coupling consistency, i.e., the reliability of coupling between fingers at the real and the artificial hand, independent of the anatomical plausibility of this coupling.

These contrary views were tested for body ownership and agency, two different aspects of the bodily self (Gallagher, 2000; Tsakiris et al., 2006; Tsakiris et al., 2007b). Two versions of the RHI paradigm were implemented, one based on passive touch and the other on active movements. In different experimental conditions, anatomical congruence and coupling consistency were systematically varied. A manipulation check, comparing synchronous against asynchronous conditions, confirmed that the experimental set-up was valid to induce an RHI, both regarding a perceptual task and phenomenal self-reports (Figure 12). For the phenomenal self-reports, enhanced RHI effects were found for the active as compared to the passive induction method, but this advantage was not reflected by the performance in the perceptual task. Furthermore, it can be inferred from Figure 12 that the pronounced effect after active movements was not due to more agreement to the items after the synchronous conditions, but rather to less agreement after the asynchronous conditions (i.e., asynchronous movements resulted in less agreement than asynchronous touches).

The results of study 4 are in line with the assumption of a congenital body-model (De Preester & Tsakiris, 2009). The comparison between anatomically congruent and incongruent feedback conditions (Figure 13) indicates that the effectiveness of the RHI depends on the anatomical congruence of the coupling between real and artificial fingers. In contrast, the comparison between consistent and inconsistent feedback conditions shows that coupling consistency, independent of anatomical congruence, has no influence on the strength of the illusion (Figure 14). These results strongly support the assumption of a congenital body-model, conform with previous reports of anatomical constraints regarding the incorporation of artificial limbs (Ehrsson et al., 2004; Holmes et al., 2006; Pavani et al., 2000; Tsakiris & Haggard, 2005), and extend them by showing that anatomical congruence is equally important for both the sense of ownership and the sense of agency. Neither regarding anatomical congruence nor regarding coupling consistency interactions with the induction methods (passive touch and active movements) have been found for any of the dependent variables. The

temporal synchrony between stimuli (or movements) at the own and an artificial hand, being a strong predictor and a necessary condition for the RHI, does not elicit the incorporation of an artificial hand, which deviates from specific *a priori* assumptions regarding body appearance and anatomy.

The notion of an invariant congenital body-model which is resistant to deviant sensory feedback (Costantini & Haggard, 2007; De Preester & Tsakiris, 2009; Tsakiris & Haggard, 2005) is further confirmed by clinical reports of phantom sensations in patients who were born without the respective limb (Brugger et al., 2000; Gallagher et al., 1998; Ramachandran, 1993). Such aplasic phantoms can persist for a life-time, notwithstanding the absence of afferent feedback from the missing limb (Melzack et al., 1997). However, alternative explanations of aplasic phantoms based on postnatal learning processes have also been raised (Price, 2006).

Another interesting result of study 4 consists in the main effect of induction method (irrespective of the experimental conditions) leading to a higher level of agreement after passive touch as compared to active movements. This main effect was exclusively found for perceived ownership and affective valence with respect to all three comparisons (Figure 12-14). Induction method had no effect on the perceptual task and on the agency items. While a greater affective valence of touches with soft paint brushes can be explained in terms of affective touch (Essick et al., 2010), it seems rather peculiar that, with respect to measures of embodiment, exclusively perceived ownership was enhanced after passive touch as compared to active movements. Subjectively perceived ownership seems to be particularly susceptible to passive tactile stimulation, regardless of whether the felt touches are asynchronous, anatomically incongruent or inconsistently combined with the seen touches at the artificial hand.

Based on evidence that the affective components of touch are processed within the insular cortex (C. McCabe, Rolls, Bilderbeck, & McGlone, 2008; H. Olausson et al., 2002; H. W. Olausson et al., 2008), a region which has also been shown to play a role in bodily self awareness (A. D. Craig, 2009; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Karnath, Baier, & Nagele, 2005), it might be speculated whether the effect on perceived ownership is mediated by insula activations. Indeed, activations in the right posterior insula

have been discussed as a neural correlate of perceived ownership over the body (Tsakiris et al., 2007a). An involvement of the insula region was also proposed for the experience of agency (Farrer & Frith, 2002), but due to the absence of any movements during the passive induction method it is well conceivable that perceived agency was unaffected. Nevertheless, it remains unexplained why the increased feeling of ownership after passive touch was not reflected by the perceptual measure of proprioceptive drift.

It has been argued that deviant visual feedback regarding efferent motor commands might be the source of pathological pain in patients with limb amputations (Harris, 1999; C. S. McCabe, Haigh, Halligan, & Blake, 2005; Moseley & Gandevia, 2005). This hypothesis is based on observations suggesting a link between aversive sensations and incongruent sensory feedback about own body movements (Fink et al., 1999) and is further supported by the fact that phantom pain can be relieved by providing the patients with congruent visual feedback regarding their intended movements with the amputated limb (Diers, Christmann, Koeppe, Ruf, & Flor, 2010; Ramachandran & Rogers-Ramachandran, 1996). Though it might be questionable whether incongruent visual feedback about own body movements really triggers pain (Moseley & Gandevia, 2005), or rather a wide spectrum of strange and maybe unpleasant sensations, as in the study by McCabe et al. (2005), a relevant question in the context of this discussion is whether negative affect is specifically associated with incongruent feedback regarding body movements or with incongruent feedback regarding bodily sensations in general.

The assessment of affective valence in study 4 enables the examination of this issue. Anatomically incongruent movements of the artificial hand significantly reduced the affective valence during the respective condition. The effect of incongruent feedback, however, was not specific for movements, but was also found for passive touch (Figure 13d). The case of incongruent sensory feedback in amputees might be reflected more precisely by the comparison between synchronous and asynchronous visual feedback, because, strictly speaking, motor commands of amputees are not accompanied by incongruent movements but by no movements at all. Nevertheless, the analysis of temporal synchrony revealed the same pattern: the significant effect of asynchronous visual feedback on

affective valence was not restricted to movements and also found for passive touch (Figure 12d).

In summary, the results from study 4 reveal a critical constraint on the plasticity of body representations. The incorporation of artificial hands into a representation of the own body within the RHI paradigm is constrained by an anatomically congruent coupling between fingers of the own and the artificial hand. The anatomical congruence is equally important for both the original version of the RHI, based on passive tactile stimulation, and a modified version, involving active motor control over the artificial hand.

The strong effect of anatomical congruence combined with the absent effect of coupling consistency, a pattern which was found for both the feeling of body ownership and agency as well as for a more indirect measure of proprioceptive drift, constitutes new evidence for the existence of a congenital body-model and provides insights concerning its impact on alterations of body representations.

6 General Discussion

Various studies have shown that the representations of the human body and the peripersonal space immediately surrounding this body are subject to extensive dynamic changes (Longo & Lourenco, 2007; Lourenco & Longo, 2009; Maravita & Iriki, 2004; Tsakiris & Haggard, 2005). For example, representations of peripersonal space can be extended and compressed, depending on short-term alterations of reaching distance (Longo & Lourenco, 2006; Lourenco & Longo, 2009). When using a rake, this reaching distance is expanded compared to a situation in which we can manipulate our environment only within arm length. As a result, far space becomes relevant for our immediate actions and the representation of the space surrounding us adjusts according to this modification (Berti & Frassinetti, 2000; Longo & Lourenco, 2006; Maravita & Iriki, 2004).

The same situation can also be described in terms of dynamic changes in body representations (Gallese & Sinigaglia, 2010). In accordance with the notion that 'the draughtsman's immediate perception seems to be of the point of his pencil, the surgeon's of the end of his knife, the duellist's of the tip of his rapier as it plunges through his enemy's skin' (James, 1890/1950, vol.2, p.37-38), tool-use has been shown to modulate the representation of the body (Cardinali et al., 2011; Johnson-Frey, 2003; Maravita & Iriki, 2004; Yamamoto & Kitazawa, 2001). According to this view, the utilization of the rake, accompanied by the feeling of controlling it, induces a change in the representation of the own body (Head & Holmes, 1911; Maravita & Iriki, 2004). This example not only shows that alterations of body representations usually coincide with alterations of spatial representations, but rather that the concepts of the body and peripersonal space are fundamentally connected to each other (Cardinali et al., 2009a; Gallese & Sinigaglia, 2010; Holmes & Spence, 2004).

The major goals of this thesis were twofold. In the first part (studies 1 and 2), it was investigated how postural body representations affect the representation of peripersonal space, while the second part (studies 3 and 4) was an attempt to identify some of the necessary and sufficient preconditions for alterations of body

representations. The present chapter will be dedicated to a discussion of the implications and conclusions which can be derived from this thesis. To provide a solid basis for this general discussion, I will summarize the main results from the studies described in the previous four chapters.

6.1 Main Results

Study 1 and 2 demonstrated that the representation of peripersonal space varies depending on alterations of body posture. By comparing tactile localization in a vertical as compared to a woven posture of the hands (Figure 1a), study 1 showed that both finger and hand processing is influenced by a postural representation of the body. Furthermore, the direction of this postural effect was modulated by the task in question, i.e., whether attention was directed to a differentiation of hand laterality or finger type. Finger processing was facilitated in the woven posture, while the processing of hands was ameliorated in the vertical posture (Figures 4 and 5).

In study 2, dynamics in the representation of peripersonal space were investigated by the comparison of tactile hand identification in an adjacent as compared to a separated posture of the hands (Figure 6a). Supplementary to a general facilitative effect of the separated posture on tactile identification of hand laterality, it was shown that the performance was modulated by the spatial distance between the tactile stimuli and the non-stimulated hand (i.e., the hand representing a different response). Reaction times towards tactile stimuli were faster with increasing distance between the spatial coordinates of a tactile stimulus and those of the non-stimulated hand (Figure 6b). The comparison between a right-enclosed and a left-enclosed posture, which were also implemented in study 2, revealed no significant differences in the performance of tactile hand identification (Figure 7).

Study 3 and 4 investigated the dynamic qualities of body representations. Keeping the veridical posture of the right hand constant, we tested the influence of visual feedback about passive tactile stimulations and active movements on the subjectively

perceived posture of the right hand. In study 3, we found that both the passive and the active induction method of the RHI were capable of eliciting a strong subjective feeling of ownership over an artificial limb. These phenomenal self-reports were accompanied by a significant proprioceptive drift of the own towards the artificial hand, as measured by means of a perceptual task and a motor task (Figure 10). Further important results of study 3 consisted in a higher proprioceptive drift after active movements as compared to passive touch, which was specific for the performance in the motor task and absent for phenomenal self-reports and perceptual responses. Furthermore, and again specific for the motor task, the differences between synchronous and asynchronous feedback did not correlate between the passive and the active induction method (Table 7). These results suggest a fundamental distinctiveness of motor responses compared to perceptual responses and phenomenal self-reports, which has important implications for the implementation of motor tasks as well as for the interpretation of respective findings.

In study 4 we examined the influence of anatomical congruence regarding the visual feedback within the RHI on the incorporation of an artificial limb. For both the passive and the active induction method, it was found that anatomically incongruent feedback (i.e., reversed coupling of index and middle fingers of the own and the artificial hand) abolished the subjectively perceived incorporation of the artificial hand. The impact of anatomical congruence was confirmed by a perceptual measure of proprioceptive drift as well as by ownership-related and agency-related questionnaire items (Figure 13). Study 4 also investigated the importance of coupling consistency (i.e., the reliability of the coupling between real and artificial fingers), but for both passive touch and active movements, no influences were found, neither regarding the perceptual task nor the phenomenal self-reports (Figure 14).

6.2 Discussion and Implications

The representations of body and peripersonal space are closely linked (Cardinali et al., 2009a; Holmes & Spence, 2004). This is clearly acknowledged by the fact that the concept of peripersonal space is defined with strict reference to the bodily borders, i.e., as the space immediately surrounding the body (Legrand et al., 2007; Làdavas & Farnè, 2004; Makin et al., 2008). Consequently, alterations of body representations should coincide with alterations of the representation of peripersonal space. An increase in the represented arm length, which is discussed as an effect of tool-use (Cardinali et al., 2011; Head & Holmes, 1911; Johnson-Frey, 2003; Maravita & Iriki, 2004), also extends the space surrounded by the represented body (Gallese & Sinigaglia, 2010).

The results of this thesis reveal new evidence for the interdependency of body and space representations. Study 1 and 2 showed that modifications of the postural representation of the body (by varying body posture) induce changes in the representation of peripersonal space. Dependent on the hand's posture, tactile stimuli were processed differently. Conversely, study 3 and 4 confirmed, in accordance with previous studies on the RHI, that the spatial displacement of visual feedback concerning tactile stimuli affects the postural representation of the body.

These findings are in line with theoretical assumptions about the interrelation between the representations of body and peripersonal space (Cardinali et al., 2009a; Làdavas & Farnè, 2004) and extend previous insights into this issue (Holmes & Spence, 2004; Overvliet et al., 2011; Shore et al., 2005; Spence et al., 2004). Study 1 provides a framework for a thorough description of peripersonal space representations in terms of response fields. This concept, which was further elaborated in study 2, accounts for a variety of observations concerning the localization of tactile stimuli within an external frame of reference (Driver & Grossenbacher, 1996; Lloyd, 2007; Shore et al., 2005; Soto-Faraco et al., 2004) and inspired a reinterpretation of the results of Haggard et al. (2006) regarding the spatial representations of fingers and hands. Study 3 and 4 corroborate previous findings on the influence of spatially displaced visual feedback of tactile stimuli on alterations of postural body

representations by illuminating necessary and sufficient preconditions for these alterations.

Before addressing the dynamic qualities of body and space representations, an issue raised by several authors needs to be considered: if representations of the body and of peripersonal space are so fundamentally linked, why do we need separate concepts for these representations, and wouldn't it be appropriate to integrate these concepts into a single one (Cardinali et al., 2009a; Holmes & Spence, 2004)? Though there is no ultimate answer to that question to date, there are possibilities which might resolve this issue in the future. One of these possibilities consists in the discovery of empirical dissociations between the representations of body and peripersonal space. For example, Cardinali et al. (2009a) speculated about alterations of peripersonal space representations accompanied by a non-altered body-schema, which might be induced by active motor control over body-extraneous objects in far space. Such an experimental modulation, so the authors argue, should affect the representation of the space relevant for immediate self-generated actions, but not the representation of the body, because anatomical constraints concerning the connectedness of body parts would be violated (Pavani et al., 2000; Tsakiris & Haggard, 2005). The experimental set-up, developed and validated in study 3 and 4 of this thesis, constitutes a suitable basis for testing this specific prediction, because the movable artificial hand can easily be placed far away from the participants, without any limitations concerning the synchrony of voluntary movements of the real and the artificial hand (see section 6.2.5).

6.2.1 Dynamics of Spatial Representations and the Concept of Response Fields

Based on the results of study 1 and 2, response fields are proposed as a conceptual framework for the description of peripersonal space representations. Specific spatial areas within peripersonal space (defined by the position of certain body parts) receive more attentional resources than others. For example, the

space immediately surrounding the hands (often referred to as near-hand or peri-hand space) is overrepresented, because it is more relevant for immediate behavior than more remote areas (Làdavas et al., 1998; Makin et al., 2007; Reed et al., 2006; Reed et al., 2010).

The concept of response fields states that peripersonal space is represented as a conglomeration of discrete spatial components, which are weighted according to their relevance for a specific task. Regarding tactile identification of body parts, this segmentation of peripersonal space facilitates the association between tactile stimuli, localized within one of these segments (i.e., with respect to an external reference system), and the specific body parts, by which they are defined. In this vein, assigning a tactile stimulus to the touched body part only requires the distinction of discrete spatial areas in peripersonal space, and the localization of the stimulus within one of these response fields.

The concept of response fields can explain a variety of experimental findings (e.g., those reported by Driver & Grossenbacher, 1996; Haggard et al., 2006; Shore et al., 2005; Soto-Faraco et al., 2004; Zampini et al., 2005). The processing of tactile stimuli should be ameliorated with a higher distance between response fields, which was found in experiment 1 of study 2 and in several other studies (Driver & Grossenbacher, 1996; Gallace & Spence, 2005; Shore et al., 2005; Soto-Faraco et al., 2004). Furthermore, reports of an impaired discrimination between tactile stimuli at the right and the left hand, when hands are interleaved (Haggard et al., 2006; Zampini et al., 2005) can be accounted for by an overlap of the respective response fields (study 1 and 2). Figure 8b depicts the response fields for the right and the left hand for several postural conditions.

In the present thesis, response fields in peripersonal space have been investigated with respect to the tactile domain. There is evidence that response fields are also applicable within other sensory modalities and might be a useful approach to understand the mechanisms of multisensory integration in peripersonal space (e.g., Lakens, Schneider, Jostmann, & Schubert, 2011; Lloyd, 2007). For example, Lloyd (2007) systematically varied the spatial distance between the participants' real hand and an artificial one in the RHI and found that the subjective perception of spatial identity of visual and tactile stimuli vanished gradually with higher distances. This

result can be described in terms of visuo-tactile response fields. The strength of the RHI could be described as a function of the degree of overlap between the response fields for the artificial and for the real hand.

An essential step in the future research on response fields therefore consists in the question as to whether the processing of visual stimuli in peripersonal space can be described in terms of response fields. A possible approach for this venture might consist in the replication of study 1 and 2, applying visual instead of tactile stimuli, or systematically varying both.

6.2.2 Dynamics of Body Representations

The role of a congenital body-model As illustrated in the introduction of this thesis, spatial representations of the body exhibit a high degree of plasticity (Botvinick & Cohen, 1998; Ehrsson et al., 2007; Guterstam et al., 2011; Longo & Lourenco, 2007; Schaefer et al., 2007; Schaefer et al., 2009), but it is an debated question as to whether these alterations of body representations are primarily based on bottom-up or top-down processes. Using the paradigm of the RHI it has been shown that the temporal synchrony of tactile stimuli and visual feedback is, though a necessary, not a sufficient condition to induce a change in the representation of the body (Pavani et al., 2000; Tsakiris & Haggard, 2005). Supplementary to the reported constraints of an anatomically plausible posture of the artificial hand (Ehrsson et al., 2004; Pavani et al., 2000) and of its realistic appearance (Holmes et al., 2006; Tsakiris & Haggard, 2005), it was shown in study 4 that also the anatomically congruent coupling between single fingers of the artificial and the real hand is an important precondition for altering body representations (Figure 13).

Contrary to anatomical congruence, the consistency of the coupling between real and artificial fingers had no significant effect on body representations (Figure 14). A consistent coupling between events at the real and the artificial hand does not seem to be a sufficient factor for inducing changes in body representations. This pattern was found for the passive and the active induction method,

and it was revealed by phenomenal self-reports and a perceptual measure of proprioceptive drift. It provides new evidence for the existence of a congenital body-model (De Preester & Tsakiris, 2009; Gallagher et al., 1998; Melzack et al., 1997), involving unmodifiable constraints concerning the general appearance of the body (Holmes et al., 2006), the connectedness of its parts (Pavani et al., 2000) and, as demonstrated in study 4, the anatomically congruent coupling between events at the body surface and their perceptual effects, or between motor commands and their bodily effects, respectively (Figure 13).

This finding stands in contrast to the report of an altered topography of the primary somatosensory cortex after anatomically incongruent visual feedback regarding tactile stimuli at the little finger and the thumb (Schaefer et al., 2006). Interestingly, in the study by Schaefer et al. (2006) neuronal alterations were accompanied by a referred sensation between little finger and thumb, but not by a subjective incorporation of the artificial hand. Since this latter finding (the absence of subjective incorporation) was replicated in study 4, it implies that alterations in the topography of the primary somatosensory cortex can occur independently from the subjective embodiment of an artificial limb. In other words, one can feel a touch at a non-stimulated finger (according to the incongruent visual feedback at an artificial hand), without perceiving the same artificial hand as one's own, which ultimately would imply two different processes being in effect during the RHI. The effect of referred sensation reported by Schaefer et al. (2006) can be solely explained by visual dominance (Hecht & Reiner, 2009), whereas the subjective embodiment is based on an altered body representation, therefore being constrained to an anatomically congruent coupling.

Controlling for top-down influences Due to the growing evidence for the importance of the distinction between a sense of ownership and a sense of agency as two different aspects of the bodily self (Gallagher, 2000; Synofzik et al., 2008; Tsakiris et al., 2006; Tsakiris et al., 2010), many attempts have been made to investigate the sense of agency within the RHI paradigm. By implementing active motor control over an artificial hand, many researchers induced a feeling of agency for the latter. However, in most studies a video-image of the own ipsilateral hand (Kammers et al., 2009b; Longo & Haggard, 2009; Newport et al., 2010; Tsakiris et

al., 2006; Tsakiris et al., 2010) or a mirror reflection of the own contralateral hand (Holmes et al., 2004; Holmes & Spence, 2005; Holmes et al., 2006) were presented as 'artificial' hands and were supposed to be recognized as body-extraneous objects. This approach raises serious issues concerning the topic under investigation, namely the incorporation of body-extraneous objects, because the participants indeed are looking at their own hand (Kalckert & Ehrsson, 2012). Due to the high familiarity regarding video-images and mirrors, it is reasonable to ask, if the incorporation of a visually displaced own hand and a prosthetic hand are based on the same mechanisms (Bertamini et al., 2011; Ijsselsteijn et al., 2006), and whether the observed effects can be explained solely on the basis of top-down processes.

The results of study 3 and 4 provide a negative answer to the latter question. The experimental set-up in both studies enabled active motor control over finger movements of an artificial wooden hand, which was unambiguously recognized as body-extraneous. Nevertheless, significant differences between the synchronous and the asynchronous feedback conditions were found in study 3, both with respect to the passive and the active induction methods. These results were replicated in study 4.

The replication of RHI effects within an experimental set-up involving active control over unambiguously body-extraneous objects is an important step for the research on agency, because it rejects the possibility that the effects found with video- or mirror-based versions of the RHI are exclusively based on top-down influences (Kalckert & Ehrsson, 2012).

6.2.3 Differential Effects of Ownership and Agency

By separating the sense of body ownership from the sense of agency over bodily movements, Tsakiris et al. (2006) could show that implementing active finger movements within the RHI affected body representations in a qualitatively different manner than the original version involving only passive tactile stimulation. The sensory integration of efferent motor commands and spatially

displaced visual feedback about the produced movements resulted in a holistic change of the hand's representation, affecting the whole configuration of the hand, while the sensory integration of tactile and visual information exclusively affected the stimulated finger (Tsakiris et al., 2006).

Together with the (recently debated) hypothesis that the sense of ownership and agency might be based on independent neuronal processes (Synofzik et al., 2008; Tsakiris et al., 2010), this observation suggests that body representations might be differently affected by passive tactile sensations, inducing a sense of ownership, and active voluntary movements, supplementarily inducing a sense of agency (Tsakiris et al., 2006). However, an overall finding of study 3 and 4 consisted in absolutely equal effects of passive touch and active movements, quantified by phenomenal self-reports, perceptual judgements and motor responses (Figures 10 and 12-14). These unexpected results will be discussed with respect to the body image/schema distinction and the impact of a congenital body-model.

Body image vs. body schema According to the initial conceptualization by Head & Holmes (1911), the body image is defined as the sum of conscious perceptions and attitudes towards one's own body, while the body schema refers to a pre-conscious representation of the body underlying the execution and guidance of movements (Gallagher, 2005). The comparison of perceptual and motor tasks is therefore a widely used method to disentangle alterations of the body image and the body schema, respectively (Cardinali et al., 2011; Kammers et al., 2006; Kammers et al., 2009a; Kammers et al., 2009b). According to the results of study 3, both the passive and the active induction method affected the body image as well as the body schema, which contradicts the results of Kammers et al. (2009; 2009), who did not find any effects on motor responses for neither of the induction methods. On the other hand, behavioral effects of the RHI in motor tasks have been reported in other studies (Heed et al., 2011; Holmes et al., 2006; Kalckert & Ehrsson, 2012; Kammers et al., 2010).

These inconsistencies with respect to motor responses might be explained by the fact that body-schematic alterations are extremely short-lived (Rossetti, 1998) and might therefore be less stable than alterations of the body image (Gallagher, 2005; Head & Holmes,

1911; Paillard, 1999). In study 3, individual RHI effects were correlated between both induction methods for all measures except the motor task (Table 7). The exclusive absence of this correlation for motor responses affirms the interpretation that effects on the body schema, as quantified by the performance in a motor task, are less stable than effects on the body image.

Cardinali et al. (2011) recently argued that the implementation of motor tasks is a necessary, but not a sufficient condition to detect alterations of the body schema. They asked their participants to point towards specific locations on their right forearm, thereby indirectly indicating its perceived length. These pointing movements were biased only when the target (elbow, wrist or fingertip) was specified by a tactile stimulus, as opposed to when it was specified by naming the body part (Cardinali et al., 2011). Since the effects in the motor task in study 3 were found after a verbal specification of the target (i.e., the right index finger), it is plausible to ask whether they would have been more pronounced after tactile target specification. The results of Cardinali et al. (2011) raise doubts on the appropriateness of the method for target specification used in study 3, and indicate an important modification to be investigated in future research.

Congenital body-model The results of study 4 revealed a strong influence of a congenital body-model, imposing anatomical constraints on alterations of body representations. Again, these influences were absolutely equal for the passive and the active induction method. Both with respect to passive touch and active movements, not only the temporal synchrony, but also the anatomical congruence between touches/movements at the real and the artificial hand was of essential importance for the induction of the RHI.

The comparability of effects resulting from the passive and the active induction method suggests a common neural basis underlying the experience of ownership and agency, as it is mandatory in an additive model of body ownership and agency (Tsakiris et al., 2010). Such an additive model proposes an asymmetrical relationship between the sense of ownership and the sense of agency. According to this view, agency necessarily includes ownership, but not vice versa (Tsakiris et al., 2006; Tsakiris et al., 2010). The alternative model, labeled as independence model, states that ownership and agency are qualitatively different experiences based on (at least

partially) different neural networks (Synofzik et al., 2008; Tsakiris et al., 2010).

It should be mentioned here that the results of Tsakiris et al. (2006) can be interpreted in accordance with a higher impact of a congenital body-model for an active version of the RHI. In their study it was reported that ownership over a specific part of an artificial hand (e.g., the index finger) can be induced independently from the perceived ownership over the residual artificial hand (e.g., the little finger). A shift of the perceived location of the stimulated finger, but not for other fingers of the same hand clearly constitutes a violation of anatomical constraints for body posture, because the finger is felt at a different spatial location than the associated hand. These violations of anatomical constraints were only found for the induction method based on passive touch, while the induction method involving active movements resulted in a holistic shift of the whole hand, i.e., according to the assumptions of a congenital body-model. The results of Tsakiris et al. (2006) therefore might be interpreted in terms of a higher impact of a congenital body-model for the active induction method, which contradicts the results found in study 4 of this thesis.

6.2.4 Methodological Aims

Methodological aims of the present thesis comprised the implementation of an RHI version involving active motor control over unambiguously body-extraneous objects, as well as the development of a new procedure for the assessment of proprioceptive drift. Both the experimental set-up and the method of assessing proprioceptive drift were successfully implemented and validated.

Experimental set-up An essential shortcoming of most studies investigating the sense of agency within the RHI consists in the use of video images of the own ipsilateral hand or mirror reflections of the own contralateral hand as ‘artificial’ hands (Holmes et al., 2004; Holmes & Spence, 2005; Holmes et al., 2006; Kammers et al.,

2009b; Longo & Haggard, 2009; Tsakiris et al., 2006; Tsakiris et al., 2010). This approach raises serious concerns as to whether the RHI effects can be accounted for solely on the basis of top-down processes (discussed in section 6.2.2).

These concerns were eliminated in study 3, where participants were confronted with a prosthetic wooden hand containing movable joints at the digits, which unambiguously was recognized as body-extraneous. Movable wooden hands were also used in a recent study by Kalckert & Ehrsson (2012), but an important advantage of the method implemented here is that the movements of the artificial fingers were electronically controlled via capacitive sensors beneath the participants' own fingers (see method sections 4.2 and 5.2 for details), while in the study by Kalckert & Ehrsson (2012), artificial fingers were physically connected with the participants' own fingers. This set-up, however, involves force feedback from the artificial fingers to the own fingers, and therefore includes the risk of mingling the effects of incorporation of artificial hands and tool-use (De Preester & Tsakiris, 2009). The phenomenal experience of mechanically transmitted feedback from a tool is located at the tip of that tool rather than at the hand holding it, but this does not coincide with a feeling of 'being' the tool (James, 1890/1950; Yamamoto & Kitazawa, 2001).

The induction method developed in the present thesis does not involve a physical connection between the own and the artificial hand, and allows for more naturalistic movements of the own hand without force feedback. It therefore provides a valuable instrument to investigating the sense of agency over unambiguously body-extraneous objects. Furthermore, it constitutes an improvement over other induction methods, because it is applicable to specific research questions, which are difficult to be approached with video-based or mirror-based versions of the RHI, e.g., the issue of anatomically incongruent motor control, as it was investigated in study 4.

Assessment of proprioceptive drift A new procedure for the assessment of proprioceptive drift (i.e., a drift of the perceived position of the own hand) was developed, based on the calculation of psychometric functions regarding the perceived hand location. A thorough description of this procedure is given in the method sections of study 3 and 4 (sections 4.2 and 5.2). Apart from being validated as a reliable tool to measure the proprioceptive drift of the

own towards the artificial hand, an effect that has been consistently found in the RHI (Botvinick & Cohen, 1998; Kammers et al., 2009a; Tsakiris & Haggard, 2005), the developed procedure exhibits some essential advantages compared to alternative methods.

Most importantly, it allows for the statistical estimation of discrimination performance, which can be quantified by the slopes of the psychometric functions (Figure 11). Altered discrimination performance reflects an essential aspect with the RHI, because it indicates an increased uncertainty regarding the veridical position of the own hand. In the psychometric study by Longo et al. (2008), a perceived 'loss of own hand' was revealed as a main component of the subjective experience during the RHI, and the assessment of discrimination performance might serve as a more objective measure of this subjective experience.

An alternative method for the assessment of proprioceptive drift consists in placing a ruler above the unseen hand and asking the participant to name the number, which is located directly above the own index finger (e.g., Tsakiris et al., 2006). This method requires different random sequences of numbers on the ruler as well as variations in the ruler's offset for every new application, in order to eliminate the risk of thoughtless repetitions. This inevitably causes differences between single trials, enhancing the likelihood of artefacts. In another method an object is moved visibly along a horizontal line in front of the participant, who is instructed to indicate when the perceived position of the own index finger is reached (e.g., Kammers et al., 2009a). Estimates for this method are biased towards the starting point of the movement (Riemer, Trojan, Kleinböhl, & Hölzl, 2012), so that the method requires at least two applications for each experimental condition (including left-to-right and right-to-left movements).

Due to the annihilation of the disadvantages inherent in other methods and the availability of a parameter for discrimination performance, the developed procedure constitutes a viable tool for the assessment of proprioceptive drift and discrimination performance within the RHI.

One disadvantage of the developed procedure consists in the time required for its execution, which encompassed approximately 2min. This raises the question about the temporal persistence of the RHI and the time course of the illusions strength, though the results from study 3 and 4 suggest the stability of the illusion at least over a

temporal period of the 2min. Nevertheless, this issue can be resolved in future applications of the procedure by the implementation of adaptive presentation strategies.

6.3 Conclusion

It has long been acknowledged that the mental representation of peripersonal space is fundamentally connected to the mental representation of the own body. In philosophy, this basic link has been recognized for logical reasons: a prerequisite for the perception of space is a first-person perspective, which (phenomenally) lies within the bodily borders (Blanke & Metzinger, 2009). The body itself constitutes a spatial extension of the phenomenal self (Sartre, 1943/1958).

As discussed in section 6.2.1, psychological sciences have brought forward empirical evidence for the interdependency of body and space representations. In the first part of this thesis (study 1 and 2), it was shown that postural representations of the body affect the representation of peripersonal space. Furthermore, response fields were proposed as a conceptual framework to describe changes in peripersonal space depending on body posture. The concept of response fields was developed and tested in the first part of the thesis.

The second part of the thesis (study 3 and 4) revealed some limitations regarding the plasticity of body representations, which can be induced by manipulating the perceived location of touches or bodily movements in peripersonal space. Besides the reinforcement of results from prior studies by eliminating the possibility that those were merely based on top-down processes (study 3), the impact of anatomical constraints for body representations was shown.

Overall, the results of the thesis are in line with the general notion of the interdependency between mental representations of peripersonal space and mental representations of the own body. However, although it is impossible to investigate the representation of space under conditions of an absent body, as it is symbolized in the initial excerpt on the discarnate spiritual being (Brod, 1916), the

application of tactile body illusions provides a viable tool for the research on the dynamics of body and space representations.

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Selbständigkeitserklärung

Hiermit versichere ich ehrenwörtlich, dass ich die vorliegende Arbeit selbständig und ohne unzulässige Hilfe verfasst habe. Alle Textstellen, die nach ihrem Wortlaut oder gemäß ihrem Sinn anderen Werken entnommen sind, sind als solche kenntlich gemacht.

Martin Riemer Mannheim, den 14. November 2012